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Behavioral responses of Brazilian free-tailed bats (*Tadarida brasiliensis*) to noctuid moth migrations

Jennifer Joy Krauel

University of Tennessee - Knoxville, jkrauel@utk.edu

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I am submitting herewith a dissertation written by Jennifer Joy Krauel entitled "Behavioral responses of Brazilian free-tailed bats (*Tadarida brasiliensis*) to noctuid moth migrations." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Gary F. McCracken, Major Professor

We have read this dissertation and recommend its acceptance:

James Fordyce, Susan Reichert, Scott Stewart

Accepted for the Council:

Dixie L. Thompson

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

**Behavioral responses of Brazilian free-tailed bats (*Tadarida
brasiliensis*) to noctuid moth migrations**

**A Dissertation Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville**

**Jennifer Joy Krauel
August 2014**

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DEDICATION

I dedicate this dissertation to the memory of my parents, Ernest and Joy Krauel.

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ABSTRACT

Animal migrations involve significant movement of biomass across landscapes and are likely to have cascading effects on animal and plant communities. However, most studies on migration address the behavior and ecology of single taxa, such as birds or insects. Few consider more than one trophic level or predator/prey interaction within the overall migration context. I studied the migration ecology of noctuid moths and of Brazilian free-tailed bats in Texas. Noctuid moth migrations during the 2010-2012 fall seasons were driven significantly by weather at the regional and local levels. Bats also responded to the same weather patterns, with changes in body mass and bat flight activity linked to increased northerly wind after cold front passage. Many of the behavioral and physiological changes in bats were more likely due to their own migratory cycles, rather than in direct response to the local availability of migratory moths in the study area. Noctuid moths are destructive agricultural pests affecting crops on a continental scale, and the bats offer significant pest control ecosystem services. Since the system is driven by weather, understanding the system is important because it is likely to be affected by climate change.

PREFACE

This is love: to fly toward a secret sky, to cause a hundred veils to fall each moment. First to let go of life. Finally, to take a step without feet.

Rumi

He has a gift for you, but it has no name.

It is windy and woolly.

He holds it in the moonlight, and it sings

Like a newborn beast,

Like a child at Christmas,

Like your own heart as it tumbles

In love's green bed.

You take it, and he is gone. — Mary Oliver

But it's mine, this poem of the night,

and I just stood there, listening and holding out

my hands to the soft glitter

falling through the air. I love this world,

but not for its answers.

— Mary Oliver

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INTRODUCTION

Animal migrations involve significant movement of biomass across landscapes and are likely to have cascading effects on the animal and plant communities therein (Yang et al. 2008; Mooney et al. 2010; Semmens et al. 2011; Bauer and Hoyer 2014). However, most studies approach migration from the perspective of explaining behavior or ecology of a single taxa or group of similar taxa, such as birds (Rubenstein et al. 2002; Faaborg et al. 2010; Schmaljohann et al. 2012; Rolshausen et al. 2013) or insects (Bale and Hayward 2010; Chapman et al. 2011; Stefanescu et al. 2013). Few studies (Sanchez-Zapata et al. 2007; Alerstam et al. 2011; Cortes-Avizanda et al. 2011) consider more than one trophic level or predator/prey interaction within the overall migration context (Dingle 2006).

This study attempts to address this gap in understanding through study of the migration ecology of noctuid moths and of Brazilian free-tailed bats (*Tadarida brasiliensis*) in Texas, USA. In the chapters that follow, I test the following hypotheses:

1. Changes in noctuid moth numbers are linked to changes in regional and local meteorological patterns
2. Bat flight activity and changes in body mass are linked to the same weather patterns
3. Bats alter foraging patterns to take advantage of increased levels of migratory moth abundance
4. Bats shift echolocation call parameters with altitude and levels of migratory moth abundance

Chapter 1 (Krauel and McCracken 2013) is a literature review of recent trends in bat migration research, and was included in the 2013 book, *Bat Ecology, Evolution, and Conservation*. Chapter 2 introduces the main study area and organisms, and addresses the first two hypotheses listed above. Chapter 3 applies the moth dataset described in Chapter 2 to studies of bat foraging activity at different altitudes during moth migration events, to address the last two hypotheses listed above.

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CHAPTER I

RECENT TRENDS IN BAT MIGRATION RESEARCH

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Abstract

In this chapter we discuss the state of research on bat migration and compare some of these patterns to those of birds. We begin with an overview of the literature on migration, apply migration theory, and discuss case studies on four bat species on which the greatest knowledge and understanding of migratory patterns exists. We also discuss what is known of motivating factors for bat migration and where research needs are apparent.

About Migration

Migration is the movement of animals that are following seasonal availability of resources and strategies involve an astonishing variety of schemes. Birds and mammals differ from insects in migration: individual birds and mammals can do many round trips, usually reproducing only once per trip (but see Rohwer *et al.* 2009), whereas insects typically undergo multiple generations per migratory cycle (Drake and Gatehouse 1995). Dingle (1996) asserted that migrating animals display some or all of the following characteristics: (1) traveling longer distances and in relatively straighter lines than during foraging, (2) displaying special predeparture or postarrival behaviors such as hyperphagia, (3) storing energy to use during or after the trip, and (4) not displaying normal responses to stimuli such as pheromones or prey. Migration differs from dispersal, which is generally unidirectional.

Understanding animal migration is important. Migratory animals include wild birds that span political borders and spread zoonotic disease that can affect humans. Understanding animal migration is important. Migratory animals include wild birds that span political borders and spread zoonotic disease that can affect humans (Altizer *et al.* 2011; Calisher *et al.* 2006) and agricultural insect pests such as the corn earworm (*Helicoverpa zea*) which cause billions of dollars of economic damage. Migratory bats help suppress those migratory pests (Lee and McCracken 2005). The migratory lesser long-nosed bat (*Leptonycteris curasoae*,

Fleming 2004), and the straw-colored fruit bat (*Eidolon helvum*, Richter and Cumming 2008) are important pollinators and seed dispersers that follow seasonal blooms of flowers and fruit for thousands of km across international borders. Moving animals transfer energy and nutrients among ecosystems with effects that are poorly studied, if at all (Wikelski *et al.* 2007). Migratory animals also face increasing pressures, such as habitat fragmentation and climate change, which are likely to disrupt poorly understood systems, with unpredictable results (Sherwin 2012; Wilcove and Wikelski 2008). In the worst cases, pressures combine. For example, increasing reliance on wind energy is promoted to meet demands for energy and counter climate change, and yet wind turbines kill bats and most bats killed are migratory (Arnett *et al.* 2008). Even given adequate conservation resources, it is difficult to protect what is not understood.

Overview of migration in bats

With a current estimate of at least 1133 species worldwide (Reeder *et al.* 2007), bats represent about a quarter of all mammalian diversity. There are several reviews covering migration in bats (Cryan and Veilleux 2007; Fenton and Thomas 1985; Fleming and Eby 2003; Griffin 1970; Hutterer *et al.* 2005; Popa-Lisseanu and Voigt 2009), and current literature identifies at least 87 species in 10 families in which all or part of the species population may undergo regional or long-distance migration (Table 1). This is likely a small representation of bats that actually migrate. Much migration research has been devoted to birds (Faaborg *et al.* 2010) with relatively little known about migration in bats. While bird and bat migration have similarities based on Dingle's (1996) characteristics, there appear to be some significant differences in scale and behavior. First, migration in bats is much less common than in birds, perhaps because most birds do not hibernate to escape extremes of weather (Brigham *et al.* 2012; Woods and Brigham 2004). Second, bat migration tends to involve shorter distances and possibly shorter intervals between stopovers. No bat species undergoes the globe-spanning ranges of birds such as the arctic tern; the longest documented bat movements are about 2,000 km (Fleming and Eby 2003). Third, bats apparently forage along the way, while birds often cover hundreds of km without stopping or feeding.

Bats migrate to follow two types of resources, roosts and food (Fleming and Eby 2003). In temperate areas, some bats move regionally (100-500 km each way) in search of roosts with suitable characteristics for hibernation (Rodrigues and Palmeirim 2008). Long-distance (>1,000 km) migrating bats in temperate areas often forgo hibernation by wintering in areas with milder climates offering food (Fleming and Eby 2003), although some European bats undergo long migrations to preferred hibernacula (Hutterer *et al.* 2005). In tropical or sub-tropical areas, long-distance migrants follow transient fruit or nectar resources, often in

Table 1.1. Bats known to migrate or suspected of migration.

Family	Species	Dis- tance	Reference
Molossidae	<i>Eumops perotis</i>		Medellin 2003
	<i>Eumops underwoodi</i>		Medellin 2003
	<i>Mops condylurus</i>		McGuire and Ratcliffe 2011
	<i>Nyctinomops macrotus</i>	L	Medellin 2003
	<i>Otomops madagascariensis</i>		CMS 2012
	<i>Otomops martiensseni</i>		CMS 2012
	<i>Tadarida brasiliensis</i>	1800	Cockrum 1969
	<i>Tadarida insignis</i>		Funakoshi and Yamamoto 2001
	<i>Tadarida latouchei</i>		CMS 2012
	<i>Tadarida condylura</i>		O'shea and Vaughan 1980
	<i>Tadarida bennettii</i>		O'shea and Vaughan 1980
	<i>Tadarida pumila</i>		O'shea and Vaughan 1980
	<i>Platymops setiger</i>		O'shea and Vaughan 1980
Phyllostomatidae	<i>Anoura geoffroyi</i>		Medellin 2003
	<i>Carollia perspicillata</i>	<200	Fleming 1988
	<i>Choeronycteris mexicana</i>	L	Valiente-Banuet et al. 1996
	<i>Leptonycteris curasoae</i>	>1000	Cockrum 1991
	<i>Leptonycteris nivalis</i>	>1000	Moreno-Valdez et al. 2004
	<i>Leptonycteris sanborni</i>		Cockrum 1991
	<i>Platalina genovensium</i>		CMS 2012
	<i>Sturnira lilium</i>		Mello et al. 2008
Vespertilionidae	<i>Antrozous pallidus</i>	R	Medellin 2003
	<i>Barbastella barbastellus</i>	290	Hutterer et al. 2005
	<i>Eptesicus fuscus</i>		Medellin 2003
	<i>Eptesicus nilssonii</i>	450	Hutterer et al. 2005
	<i>Eptesicus serotinus</i>	330	Hutterer et al. 2005
	<i>Laio</i>		McGuire and Ratcliffe 2011
	<i>Lasionycteris noctivagans</i>	U	Cryan 2003
	<i>Lasiurus borealis/blossevillii</i>	U	Cryan 2003
	<i>Lasiurus cinereus</i>	U	Cryan 2003

Table 1.1. Continued.

Family	Species	Dis- tance	Reference
	<i>Lasiurus ega</i>		Medellin 2003
	<i>Lasiurus intermedius</i>		Medellin 2003
	<i>Lasiurus seminolus</i>	U	Perry et al. 2010
	<i>Lasiurus xanthinus</i>		Medellin 2003
	<i>Myotis auriculus</i>		Medellin 2003
	<i>Myotis blythii</i>	488	Hutterer et al. 2005
	<i>Myotis brandtii</i>	618	Hutterer et al. 2005
	<i>Myotis californicus</i>		Medellin 2003
	<i>Myotis capaccinii</i>	140	Medellin 2003
	<i>Myotis chiloensis</i>		Fleming and Eby 2003
	<i>Myotis ciliolabrum</i>		Medellin 2003
	<i>Myotis dasycneme</i>	350	Medellin 2003
	<i>Myotis daubentonii</i>	304	Hutterer et al. 2005
	<i>Myotis evotis</i>		Medellin 2003
	<i>Myotis griescens</i>	>500	Tuttle 1976
	<i>Myotis lucifugus</i>	>500	Fleming and Eby 2003
	<i>Myotis myotis</i>	436	Hutterer et al. 2005
	<i>Myotis mystacinus</i>	240	Hutterer et al. 2005
	<i>Myotis nattereri</i>	327	Hutterer et al. 2005
	<i>Myotis sodalis</i>	500	Fleming and Eby 2003
	<i>Myotis thysanodes</i>		Medellin 2003
	<i>Myotis tricolor</i>		O'shea and Vaughan 1980
	<i>Myotis velifer</i>		Medellin 2003
	<i>Myotis volans</i>		Medellin 2003
	<i>Myotis yumanensis</i>		Medellin 2003
	<i>Nyctalus lasiopterus</i>	U	Hutterer et al. 2005
	<i>Nyctalus leiseri</i>	1568	Hutterer et al. 2005
	<i>Nyctalus noctula</i>	1546	Hutterer et al. 2005
	<i>Perimyotis subflavus</i>	R	Fleming and Eby 2003
	<i>Pipistrellus nathusii</i>	1905	Hutterer et al. 2005
	<i>Pipistrellus pygmaeus</i>	U	Hutterer et al. 2005
	<i>Pipistrellus pipistrellus</i>	1123	Hutterer et al. 2005
	<i>Scotoecus hindei</i>		O'shea and Vaughan 1980
	<i>Scotophilus nigrita</i>		O'shea and Vaughan 1980
	<i>Vespertilio murinus</i>	1787	Hutterer et al. 2005

Table 1.1. Continued.

Family	Species	Dis- tance	Reference
Minio- pteridae	Miniopterus australis		McGuire and Ratcliffe 2011
	Miniopterus inflatus		McGuire and Ratcliffe 2011
	Miniopterus natalensis		Miller-Butterworth et al. 2003
	Miniopterus schreibersi	833	Hutterer et al. 2005
Emballon- nuridae	Emballonura monticola		CMS 2012
	Emballonura semicaudata		CMS 2012
	Taphozous mauritanus		O'shea and Vaughan 1980
	Taphozous melanopogon	200	Gopalakrishna 1986
Ptero- podidae	Eidolon helvum	1500	Thomas 1983
	Epomorphorus wahlbergi		McGuire and Ratcliffe 2011
	Myonycteris torquata	750	Thomas 1983
	Nanonycteris veldkampii	750	Thomas 1983
	Pteropus alecto	U	Breed et al. 2010
	Pteropus poliocephalus	978	Ratcliffe 1932
	Pteropus scapulatus		Ratcliffe 1932
	Pteropus vampyrus		Epstein et al. 2009
Hipposi- deridae	Hipposideros commersoni		O'shea and Vaughan 1980
	Hipposideros lankadiva	475	Gopalakrishna 1986
	Triaenops persicus		O'shea and Vaughan 1980
Rhinolo- phidae	Rhinolophus landeri		O'shea and Vaughan 1980
	Rhinolophus hildebrandti		CMS 2012
Megader- matidae	Cardioderma cor		O'shea and Vaughan 1980
Rhinopo- matidae	Rhinopoma microphyllum	900	Gopalakrishna 1986

Note that this does not represent all migratory bats, nor has migration necessarily been confirmed for each of these species. Where available, longest documented one-way migration distance is listed in km; L = known long distance migrant, R = known regional migrant, U = maximum distance stated as unknown in literature, blank indicates no distance information available.

response to wet versus dry seasons (Fleming and Eby 2003). There are as yet no studies that examine whether insect-eating bats migrate in response to seasonally available prey. Perhaps seasonal movements in pursuit of prey are obscured in north-south (latitudinal) migrants by the current lack of almost any information on the seasonal availability of insects beyond those considered agricultural pests. While it may be fair to assume that regional migrants move longitudinally or even in seemingly random directions in search of roost sites (Griffin 1945, 1970; Tuttle 1976), many latitudinal migrants may be in pursuit of insects or other food, with available roosts being an additional or secondary factor.

Migratory behavior appears to have evolved multiple times independently, especially in the western hemisphere (Bisson *et al.* 2009; Popa-Lisseanu and Voigt 2009). Because large fluctuations in resources are less pronounced in the tropics than in temperate regions, and the greatest diversity of bats is in the tropics and most bat species likely originated there, migration of bats in temperate regions is likely to be an evolved rather than ancestral trait (Fleming and Eby 2003). Although migratory behaviors in bats are probably less diverse than in birds, some patterns are emerging. For example, there are many instances of sex-based migration (Fleming and Eby 2003; Ibanez *et al.* 2009), with females moving farther north in the spring in North America (Cryan 2003 but see Kurta 2010) as well as in Europe and Australia (Fleming and Eby 2003). Bats have been observed to migrate in groups, sometimes even mixed-species groups (Cryan and Veilleux 2007; Fleming and Eby 2003). In some bats, migration coincides with mating behavior (Cryan and Veilleux 2007). Migratory bats typically share similar morphology such as high wing aspect ratios and high wing loading (Norberg and Rayner 1987) that facilitate high-speed flight over long distances. However, behavioral and morphological characteristics likely facilitated the evolution of migration, rather than being a causal agent for its evolution (Fleming and Eby 2003).

As in birds and other taxa, Bisson *et al.* (2009) suggest that migration evolved independently in several lineages in the large bat family Vespertilionidae. Within the Vespertilionidae, many cave-roosting species of *Myotis* are regional migrants but none are long distance migrants. In contrast, many species of *Lasiurus*, which roost in trees, are long-distance migrants, but based on current knowledge none appear to be regional migrants. Thus, Bisson *et al.* (2009) conclude that long distance migration is significantly less likely to have evolved in cave than tree roosting bats. Bisson *et al.* (2009) suggest that migration in this group of bats evolved differently than in birds, which started with short- then stepped up to long-distance migration. However, Berthold (1999) posits that the most likely scenario to explain the evolution of migration in birds is the coexistence of both migratory and non-migratory genes in the same population, which are expressed

depending on a threshold variable, and he suggests this model may be ancestral to birds. Thus, ecology, morphology, or perhaps physiology drives evolution of migration, rather than the reverse. This hypothesis could also explain Bisson *et al.*'s (2009) results suggesting independent evolution of migration in multiple lineages of bats as necessary to track resources.

Bats are notoriously difficult to study, and tracking these small animals during seasonal movements is especially difficult. Much of what we know about patterns of bat migration comes from large-scale banding efforts conducted in the first half of the twentieth century (Cockrum 1969; Glass 1982; Griffin 1945; Hutterer *et al.* 2005; Steffens *et al.* 2007; Tuttle 1976). In these studies, more than a million bats in Europe, and hundreds of thousands of colonial cave-roosting bats in North America were captured in roosts and banded, and the small fraction of bands recovered offers clues to seasonal movements. Individual Brazilian free-tailed bats (*Tadarida brasiliensis*) banded in caves in the US Southwest show that some individuals moved 1,800 km into Mexico, at rates of about 50 km/day (Cockrum 1969; Glass 1982). In Europe, banding started in the 1940s in 7 countries and continues today in 35 countries. Data are available for 47 European species of bats and consolidation of records from across the region is ongoing (Hutterer *et al.* 2005). Even with partial results, data show a striking pattern of movement for many long-distance migrants between northeastern and southwestern Europe (Hutterer *et al.* 2005). Banding of bats in North America as well as several European countries has been largely curtailed after inappropriate practices led to massive banding-related mortality, often associated with inexperienced banders targeting winter populations of cave bats (Hutterer *et al.* 2005; Ellison 2008; but see Rodrigues and Palmeirim 2008). While banding can be harmful to bats, tracking individual bats is crucial to understanding bat migration. If possible, improvements in banding technology as well as documentation of species of bats that tolerate banding would greatly assist in this effort.

Two recent serious threats to bats both impact migratory bats, and have resulted in a resurgence of research on bat migration. First, the growing importance of wind energy as an alternative to more carbon-intensive energy sources has resulted in massive expansion of wind turbine facilities across the world. Wind turbines kill many bats, but migratory bats are the most commonly killed (Arnett *et al.* 2008). The second threat, white-nose syndrome (WNS), a disease of hibernating bats in North America, is caused by the fungus *Geomyces destructans* (Lorch *et al.* 2011). WNS has resulted in severe mortality to several species of cave-roosting bats in North America and may result in local extinctions of the once common regional migrant little brown bat (*Myotis lucifugus*) (Frick *et al.* 2010). Understanding movements of these bats, for example through analysis of genetic structure of populations, is important to predict patterns of disease spread (Dixon 2011). These concerns, as well as uncertainties about

the effects of climate change on migratory bats (Popa-Lisseanu and Voigt 2009), have spurred research to understand the causes of the mortality and possible approaches to mitigate these threats.

Applying migration theory to bats

There is considerable theoretical and integrative research on migration (Berthold 1999; Dingle 2006), but almost all treatments of migration theory ignore bats (e.g. Akesson and Hedenstrom 2007; Chapman *et al.* 2011; Dingle 2006; Hein *et al.* 2012, but see Hedenstrom 2009). This is probably because knowledge remains patchy and often even basic information remains unknown, such as which species migrate, population sizes of those species, and their migratory routes. Population sizes of North American migratory tree bats are considered by some as not measurable (Carter *et al.* 2003). While these animals are under threat by wind turbines, and even though we see evidence for population decreases (Winhold *et al.* 2008), we cannot clearly estimate the magnitude of the threat without population size estimates. Applications of molecular data offer windows to estimates of current and historical population sizes and should be explored (Russell *et al.* 2011). Also, knowledge gaps are exacerbated by current limits on tracking technology; Holland and Wikelski (2009) refer to this as the “small animal problem” where 90% of known migratory bat species cannot be individually tracked with currently existing technology. Thus, fundamental research must still be addressed before migration theory can be extended to apply to bats.

Migration appears to be a plastic behavior in many animals. In birds, substantial genetic variation for migration propensity, distance, and direction exists even in partial or non-migratory populations (Pulido 2007; Pulido 2011) and many bird species are capable of changing their migration patterns or stopping migration altogether (Sutherland 1998). For example, House Finches (*Carpodacus mexicanus*) introduced to eastern North America from a non-migratory population quickly adopted migration (Able and Belthoff 1998). Populations of Blackcaps (*Sylvia atricapilla*) that previously migrated from Europe to the Mediterranean & Africa now winter in the British Isles, probably due to milder winters and availability of bird feeders (Pulido 2007). Partial migration, where migrant and non-migrant individuals in a population share a common site during one period of their annual cycle, is common in many animal species (Berthold 1999; Chapman *et al.* 2011). Many bat species are partial migrants (Fleming and Eby 2003); in some cases (e.g. North American tree bats), males and females appear to migrate differently (Cryan 2003), and in others (e.g. Brazilian free-tailed bats), part of the population migrates and some individuals do not (Laval 1973). Moussy *et al.* (2012) review the effect of migration and dispersal on genetic

structure of populations, but much work remains to be done to understand the underlying drivers of these patterns.

Migratory birds have smaller brains than non-migrants (Sol *et al.* 2005). McGuire and Ratcliffe (2011) show that this pattern also applies to bats, and suggest that smaller brains and less mass to transport supports an energy trade-off hypothesis. Alternatively, larger brains in non-migrants may reflect selection for behavioral flexibility and the need to find food in seasonally variable habitats. This alternative hypothesis might also explain why migratory birds are less successful invaders (Sol and Lefebvre 2000). Although brain size is smaller, the hippocampus is proportionately larger in migratory birds but not in migratory bats (McGuire and Ratcliffe 2011). The hippocampus is important to spatial memory in many birds and mammals (Moser 2011). While the role of the hippocampus in bats is not currently understood, because non-migratory bats hibernate and thus avoid much of the seasonal variation in resource availability, there may be less selection and need for behavioral flexibility in bats.

Most birds fuel their migration primarily through stores of fat (Gwinner 1990). Many bats also increase fat stores before migration (McGuire *et al.* 2009; O'Shea 1976; Tuttle 1976) and researchers are beginning to examine the processes of acquiring and using fat stores, both for migration and hibernation. For example, in many mammals an increase in fat generates an increase in leptin, which results in appetite inhibition and an increase in metabolic rate (Florant and Healy 2012). In little brown bats, body mass increased before migration and hibernation, but leptin levels were low and even dissociated with fat deposition (Kronfeld-Schor *et al.* 2000; Townsend *et al.* 2008). This could explain the ability of bats to continue to add fat. In addition, a decrease in adiponectin has been linked to obesity in rodents. However, adiponectin levels decreased in tissues of fattening bats but not in circulation, indicating that weight gain in bats prior to migration and hibernation is different from pathological weight gain in other mammals (Townsend *et al.* 2008).

Researchers have suggested (Fleming and Eby 2003; O'Shea 1976; Tuttle 1976) that bats use stored fat for migration, but it is difficult to distinguish between fat used for migration and fat used for hibernation (McGuire and Guglielmo 2009) and these two uses of fat may be fundamentally different. Most mammals fuel high intensity exercise primarily through protein and carbohydrates, so the ability of mammals to use stored fat for extended endurance during migration is not well documented (McGuire and Guglielmo 2009). Actively foraging insectivorous bats use energy from harvested insects rather than stored fat (Voigt *et al.* 2010) and there is growing evidence that bats forage while migrating (Reimer *et al.* 2010; Valdez and Cryan 2009). A study of fat storage in hoary bats (*Lasiurus cinereus*), which are not known to hibernate, found differences in percent of body fat in bats captured during migration and non-migration periods, and increased expression

of enzymes indicative of conversion of stored fat to energy during migration (McGuire *et al.* 2013). Many of these differences were sex-related; females had larger fat stores and intercellular fatty acid transport structures optimized to access the fat, which may be related to females making their spring migration while pregnant (McGuire *et al.* 2013). Pregnant female hoary bats are less likely to use torpor, while males often do (Cryan and Wolf 2003) and females travel greater distances than males (Cryan 2003). Thus, females have greater migratory energetic needs. McGuire *et al.* (2013) also reported lower overall body weight in migrating than non-migrating hoary bats as well as reduced size of organs used for digestion, reducing the weight carried during migration in a manner similar to changes seen in birds making long-haul trips. Reduced digestive organs suggest that for these bats, foraging during migration is opportunistic rather than required. The combination of increased fat reserves and the ability to reduce energy needs through daily torpor is one difference between bat and bird migration strategies. Foraging during migratory periods by bats may act to “top off” fuel reserves, where birds are more likely to “empty their tanks” and completely refuel during migratory stopovers (McGuire 2012). Another intriguing difference is an increase in lung capacity in bats during migration; a lack of corresponding increase in bird lung capacity during this time may be due to constraints on bird lung structure (McGuire *et al.* 2013).

In birds, the time available for feeding to fuel migration is the main limiting factor in migration distance (Kvist and Lindstrom 2000). This results in a metabolic ceiling for storing fat despite the fact that passerine birds can migrate at night and feed by day. In one of the first attempts to include bats in a migration process model, Hedenstrom (2009) showed that since most bats neither feed nor migrate during the day, time and fueling for migration are even more constrained in bats than for birds. Hedenstrom (2009) proposes a diverging selection pressure between longer nights in autumn with increased time for feeding and transport, and lower food abundance as winter approaches, which results in an optimal migration period (Figure 1.1a). This model assumes that bats, like birds, do not forage during migration, which may not be a valid assumption. In addition, bats generally do not spend all available night hours foraging (Shiel *et al.* 1999). For example, length of night was not related to foraging time for female hoary bats, even after parturition when energy needs were high (Barclay 1989). Thus, there is no evidence that length of night is an appropriate surrogate for body condition in bats. Finally, Hedenstrom (2009) did not consider the fluctuating availability of migratory insects, which may be an important influence on the optimal date of migration (Lee and McCracken 2005; Rydell *et al.* 2010). We present an alternate model (Figure 1.1b) showing fluxes in insect availability and corresponding changes in bat foraging time; some level of body condition, perhaps defined by mass or lipid levels driven by those factors, would predict optimum migration departure time.

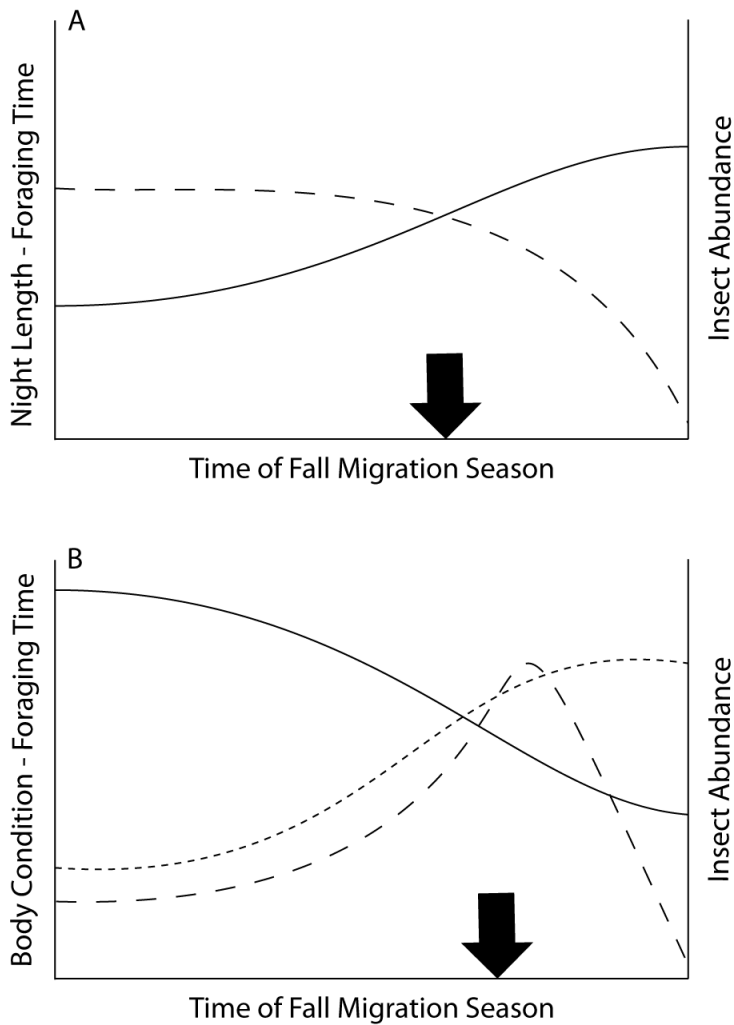


Figure 1.1. Models explaining timing of migration

In the top model (a), after Hedenstrom (2009), the solid line represents night length as an indicator of time available for foraging which we interpret as a surrogate for body condition. The dashed line represents decreasing insect abundance as the fall season progresses; the arrow indicates optimal time for maximum speed of migration. The lower model (b) represents an alternative view where insect abundance is lower at the end of summer and rises due to fluxes of migrating insects. As in the first model, the dashed line represents insect abundance, which is low at the end of the summer and then increases with the appearance of migratory insects. The solid line indicates a decrease in foraging time as insect abundance increases, and the dotted line indicates a corresponding increase in body condition. In this model, time of departure to permit optimum speed of migration is a function of body condition, which tracks insect abundance.

Animals must successfully orient their movement to arrive at a suitable destination. Birds and other animals are known to use a variety of sensory cues in orientation and navigation (Akesson and Hedenstrom 2007). This navigation is often described using the map and compass theory; i.e. determining position with respect to the goal using sensory cues (map), and determining the direction of the goal (compass). Map theory has been applied to adult avian migrants, reptiles, amphibians, and fish, and compass orientation is common in arthropods and juvenile birds (Holland 2007). Bats have good spatial memory (Holland *et al.* 2005) and Tsoar *et al.* (2011) showed that for Egyptian fruit bats (*Rousettus aegyptiacus*), multiple remote visual landmarks are important for navigation but long-distance homing probably involves at least one other mechanism. Like many animals, bats can sense earth's magnetic field (Holland *et al.* 2006). The magnetic field can provide two types of directional information: inclination, or direction toward or away from the equator, and polarity, or north/south direction. Birds are thought to respond only to inclination (Beason 2005). The preference of the Chinese noctule (*Nyctalus plancyi*) to roost in the north end of their cage suggested that unlike birds, bats respond to magnetic polarity (Wang *et al.* 2007). Bats calibrate the magnetic field using light at sunset (Holland *et al.* 2008), but while birds are thought to use polarized light at sunset for this calibration, this was not the case in bats (Holland *et al.* 2010). Bats that emerge long after sunset are presumably unable to use sunset calibration, but they also were found to not use a star compass calibrated by the geomagnetic field in place of sunset calibration (Holland *et al.* 2010). Bats appear to be responding differently to magnetic fields than birds and the ability of the eyes of nocturnal mammals to perceive polarized light remains untested.

Many animals migrate using specific routes (Dingle 1996) and there is some evidence for the use of migration routes by bats. Lesser long-nosed bats follow a specific and relatively narrow path up a resource gradient (Fleming 2004; Morales-Garza *et al.* 2007), but most migration routes used by bats are probably broader and more diffuse. Tree bats in North America seem to follow regular routes and can be netted in specific locations at specific times, but many of these observations are largely anecdotal (Cryan and Veilleux 2007; Valdez and Cryan 2009). Tree bats appear to track closer to potential roost sites along mountain ranges (Baerwald and Barclay 2009) and potentially avoid crossing open prairies. Other insectivorous bats follow linear landscape features to specific departure points before crossing open ocean (Ahlen *et al.* 2009). Migrating bats commonly follow riparian zones and shorelines (Barclay 1984; Serra-Cobo *et al.* 1998; Furmankiewicz and Kucharska 2009).

The use of stopover sites by migrating birds has received much attention (Berthold and Terrill 1991; Hedenstrom 2008) and there is growing evidence for the use of stopover sites by bats (Cryan and Brown 2007; Dzal *et al.* 2009; Taylor *et al.* 2011; McGuire *et al.* 2011). Although bats may forage en route

while migrating (Reimer *et al.* 2010; Valdez and Cryan 2009), we do not know if they remain for extended periods in particularly food-rich areas or simply forage opportunistically along the way. The definition of a migratory stopover is very scale- and species-specific (Taylor *et al.* 2011). Cryan and Brown (2007) reviewed records of hoary bats (*Lasiurus cinereus*) “stopping over” on the Farallon islands during fall migration and found that bats were present for periods of 1-35 days during the fall, but they could not show how long individual bats stayed over. Silver-haired bats (*Lasionycteris noctivagans*) have been documented stopping over during spring migration for several days at a lake in Manitoba, Canada (Barclay *et al.* 1988). Dzal *et al.* (2009) studied use by bats of a known migratory stopover site for birds at Long Point, Ontario, Canada and found both that silver-haired bats and hoary bats use Long Point as a flyway for migration, and evidence that silver-haired bats are using it as a stopover site during August. Taylor *et al.* (2011) and McGuire *et al.* (2011) tracked 30 silver-haired bats using telemetry at Long Point in fall 2009, and observed 7 “stopover flights” where the bats made flights within a 20x40 km stopover area, and 23 distinct migratory departures. However, most silver-haired bats stayed over only one night at Long Point except when weather conditions forced a delay, and most had sufficient fat reserves upon arrival at Long Point to complete their expected migration without requiring additional foraging (McGuire *et al.* 2011). Little brown bats are the most common bat at Long Point, and Dzal *et al.* (2009) found that the overall genetic diversity of captured bats during the fall migration period was higher than that found at swarming areas, suggesting that these regional migrant bats assemble at the site from diverse areas before crossing the lake. In Texas, Brazilian free-tailed bats (*Tadarida brasiliensis*) show a fall, and to a lesser extent spring, spike in their use of urban roosts use indicating possible migration stopovers (Scales and Wilkins 2007). Populations of Brazilian free-tailed bats vary at Carlsbad Cave, New Mexico, including a large temporary increase in mid-October (Altenbach *et al.* 1979; Hristov *et al.* 2010). Cockrum (1969) anecdotally reports hundreds of thousands of these bats arriving overnight at caves during migration and then departing days later, consistent with our own observations in fall at Frio Cave, Texas. Many of these caves apparently function as maternity roosts as well as migratory stopovers.

Weather has an important influence on migration for most flying animals (Shamoun-Baranes *et al.* 2010) and the influence of weather on bird migration is well documented (Able 1973; Liechti 2006; Nisbet and Drury 1968; Richardson 1990). Most nocturnal migrant birds fly in tailwinds or light winds rather than strong or head winds (Richardson 1990). Migratory bats are also more active in light winds (Arnett *et al.* 2008; Cryan and Brown 2007; Horn *et al.* 2008). In one study, hoary bats were more likely to land on an island stopover during low wind periods, low moon illumination, higher cloud cover, and to a lesser extent low barometric pressure (Cryan and Brown 2007). However, a separate study documented this species flying often in unfavorable winds (Baerwald and Barclay

2011). Silver-haired bats were less likely to leave a stopover and continue migration during rain (McGuire *et al.* 2012). There is abundant data on the timing of bird migration related to cold fronts, especially strong southward migration following cold fronts in North America when northerly winds occur with falling pressure and falling temperature (Able 1973; Richardson 1990). Bats also migrate with cold fronts (Cryan and Brown 2007). Morphology may influence these trends, however; birds with high wing loading and aspect ratio are less affected by weather variables during spring migration (Saino *et al.* 2010) and presumably there should be similar expectations for bats. Migratory insects normally fly at much slower speeds, typically 1/3 of the speed of birds and bats, but during migration insects achieve similar speeds by timing movement with favorable wind conditions (Alerstam *et al.* 2011). There is evidence that bats take advantage of concurrent migration patterns to forage on migrating insects (Lee and McCracken 2005) and even birds (Ibanez *et al.* 2001; Popa-Lisseanu *et al.* 2007).

Four examples of bat migration

To illustrate the patterns discussed above, we here describe four different examples of bat migration. Baker (1978) distinguished between facultative and obligate migrants. Facultative migrants are sensitive to local cues such as resource availability and may not undergo migration without those cues; this may explain instances of partial migration. Obligate migrants are less sensitive to cues and most individuals in a population migrate even if resources remain locally available. The hoary bat in North America is an example of a tree-roosting long distance migrant, with a primarily north-south migration route. Since hoary bats are not known to hibernate, they are a likely example of an obligate migrant. The second example, Schreiber's bent-winged bats, is another probable obligate migrant and an example of regional migrants that move seasonally in a wide variety of geographic directions between maternity and hibernacula caves. These very widespread old-world bats apparently are not negatively affected by banding (Rodrigues and Palmeirim 2008), and we summarize here the wealth of recent information connecting their behavior, population structure, and movement. Third, Brazilian free-tailed bats are included as an example of facultative migrants. Populations across North America vary widely in migratory behavior in distance, sexual bias, and direction, despite an apparent lack of genetic structure. Finally, migration of tropical bats is often quite different from migration of temperate bats. We include here the example of long-distance tropical migration in the straw-colored fruit bat, and compare that to long-distance movements of other tropical fruit bats that exhibit less typical migratory behavior.

Long distance migrant tree bats: Hoary bats

A sense of urgency for research on poorly understood long distance migration by tree-roosting bats has been motivated by the large numbers of these bats that are killed by wind turbines (Arnett *et al.* 2008). As a result, much recent research has been focused on them, for example as described in the earlier section on migration energetics. Migratory bats may be attracted to turbines (Cryan 2008; Cryan and Barclay 2009; Kunz *et al.* 2007b) especially in the autumn, and fatality rates are higher at taller turbines (Barclay *et al.* 2007). A variety of behavioral hypotheses may explain this (Cryan and Barclay 2009); for example, it could be related to North American tree bats flying at different altitudes in the fall than the spring (Cryan and Veilleux 2007; Johnson *et al.* 2011; Valdez and Cryan 2009). An alternative hypothesis posits that tree bats use large trees as landmarks during migration to aggregate socially, possibly for mating, and that they perceive wind turbines as very large dead trees (Cryan 2008). Little research has been done to test this hypothesis, but preliminary results show more hoary bat activity around cell towers than in surrounding habitats during fall migration, and these bats do not appear to be feeding (C. Willis, pers comm).

In the spring, female hoary bats move through New Mexico about a month earlier than males, and there is some evidence that they travel in groups, fly below the canopy along streams, and forage during migration (Valdez and Cryan 2009). Females are usually pregnant during spring migration and may be less likely to use torpor during this period (Cryan and Wolf 2003). Both in spring (Valdez and Cryan 2009) and fall (Reimer *et al.* 2010) the diet of hoary bats consists primarily of moths. Based on retrieved carcasses at wind energy facilities, male hoary bats passed through Alberta, Canada in late July, followed by females and young in early-mid August (Baerwald and Barclay 2011).

At wind farms in Alberta, Canada in the fall, hoary bats were recorded more often by acoustic detectors set at 30m, than by detectors at ground level or 67m above ground (Baerwald and Barclay 2011). Other studies report hoary bats flying higher in the fall than in the spring (Johnson *et al.* 2011; Valdez and Cryan 2009), although this could also be explained by bats flying too high to be detected in the spring. Hoary bats were also more likely to land on the Farallon islands during low wind speeds, as well as during low moon illumination, higher cloud cover, and to a lesser extent low barometric pressure (Cryan and Brown 2007). At the Canadian wind farm, hoary bat activity was best predicted by falling barometric pressure and this was reflected in fatality rates (Baerwald and Barclay 2011).

A comparison of acoustic detection sites on a north/south gradient across the Eastern US reveals a pattern suggestive of hoary and silver-haired bats moving north in the spring and south in the fall (Johnson *et al.* 2011), although this could also reflect variations in local foraging activity due to fluxes of insect populations.

Little is known about migratory patterns of hoary bats in other parts of its range. However, in Hawaii the bats apparently perform a seasonal altitudinal migration, with both sexes moving to lowlands during breeding season and then returning to highlands during the remainder of the year (Menard 2001). Seasonal altitudinal migration is also suggested for hoary bats in the Galapagos Islands (McCracken *et al.* 1997).

Regional migrant cave bats: Schreiber's bats

Many cave-roosting bats tend to move shorter distances, 500 km or less, and with less of a standard compass orientation than tree bats. For example, in the spring many species radiate away from common hibernacula in a star-shaped pattern (Hutterer *et al.* 2005).

The cave-roosting regional migrant Schreiber's bent-winged bat (*Miniopterus schreibersii*) is one of the most widespread bats, found throughout Europe, Africa, and Australia. Recent research reveals genetic structure between subpopulations in southeastern Europe (Bilgin *et al.* 2008), and Australia (Cardinal and Christidis 1999), and existence of the closely related *Miniopterus natalensis* in South Africa (Miller-Butterworth *et al.* 2005). Work continues on clarifying the Miniopterine phylogeny and its relationship to sister families Mollosidae and Vespertilionidae (Miller-Butterworth *et al.* 2007).

The combination of strong philopatry and extensive banding has resulted in a wealth of information on bent-winged bats including details of seasonal movements. Between 1987-2005, 36,000 bats were banded and tracked in Portugal (Ramos Pereira *et al.* 2009; Rodrigues and Palmeirim 2008; Rodrigues *et al.* 2010). These studies provide evidence of sex-biased movement, with females staging at spring roosts until just before parturition when they move to maternity roosts in caves. Following weaning of pups, they move to other caves where they spend autumn and sometimes winter. Males leave hibernacula later than females, and change roosts during maternity season. Roost temperature was much more likely to influence migration destination than insect availability (Rodrigues and Palmeirim 2008). Insect availability was inferred from temperature in foraging areas around the migratory destination, because temperature is often related to insect abundance (Rodrigues and Palmeirim 2008). These results indicate that migration of Schreiber's bats appears to be roost-driven rather than following fluctuating insect resources.

While many migratory bat species show little evidence of population structure (Petit and Mayer 2000; Russell *et al.* 2005), Schreiber's bat is an interesting exception. The extensive banding data in Portugal enable us to compare population structural patterns and observed behavior to predictive models (Ruedi

and McCracken 2009). For example, strong patterns of structure in mitochondrial DNA (mtDNA) are considered to indicate strong female philopatry to breeding sites. More diffuse patterns in mtDNA in males than in females should indicate sex-biased movement by males during breeding seasons. In this scenario, nuclear DNA (nDNA) patterns would not show structure. In the Portuguese Schreiber's bat colonies, while both males and females visit different maternity caves, all females raise pups only in the cave in which they were born (Rodrigues *et al.* 2010). Mating occurs at hibernacula shared among the colony's maternity roosts (Rodrigues and Palmeirim 2008). As a result of this strict philopatry to maternity caves, all gene flow is male-induced during regional migrations (Rodrigues *et al.* 2010). The resulting strong patterns of structure in mtDNA also appear, but at a weaker level, in nDNA in this population, reflecting the strong regional philopatry observed in both males and females (Ramos Pereira *et al.* 2009).

In a study of the closely related South African Schreibers' long-fingered bat (*Miniopterus natalensis*), Miller-Butterworth *et al.* (2003) found similar population structure. Unlike in Portugal where migration distances were smaller, in this study migratory distances varied between subpopulations. However, neither migration distance nor zoogeographic barriers were sufficient to prevent gene flow between colonies, so the observed structure was due to philopatry or other differences. In one subpopulation, morphological differences mirrored the genetic distinctions, with the northern colony showing higher wing aspect ratios than other colonies. Bats in the northern colony are intermediate migrants, traveling up to 560 km between summer and winter caves, whereas bats in other colonies travel much shorter distances (Miller-Butterworth *et al.* 2003).

Long-distance, facultative and partial migrant: Brazilian free-tailed bats

Migratory patterns of Brazilian free-tailed bats (*Tadarida brasiliensis*) are much more difficult to define than are those of the tree bats and cave bats described above. In contrast to the highly structured populations of *M. schreibersii*, populations of Brazilian free-tailed bats are panmictic, showing no genetic structure (Russell *et al.* 2005). Nonetheless, bats in different geographic areas demonstrate a variety of different migratory behaviors. In the southeastern US, they appear to be sedentary and to use torpor in winter (Cockrum 1969; Laval 1973). On the west coast of the US, bats probably migrate but not necessarily long distances or in a north-south direction (Kruttsch 1955). In mid-continent a large segment of the population are long-distance migrants, traveling as far as 1900 km between Mexico and the US (Cockrum 1969; Glass 1982). However, even in this mid-continent group of long-distance migrants, many males may remain in Mexico year-round (Davis *et al.* 1962; Glass 1982) while other males move north where they mate in the spring in Texas (Reichard *et al.* 2009).

Reports of large maternity colonies in Mexico (Lopez-Gonzalez and Best 2006) and of bats overwintering in the US (Geluso 2008; Scales and Wilkins 2007) further confuse the picture for this highly variable species.

Bats overwintering at Carlsbad cave, New Mexico included individuals of both sexes and varying ages, and evidence indicates that these bats actively feed in winter except during high winds (Geluso 2008). Banding of large numbers of bats in the 1950's and 1960's (Cockrum 1969; Glass 1982; Villa and Cockrum 1962) showed migration between caves in the southwestern United States and Mexico. For example, bats leaving nursery caves in Oklahoma range into Texas and Mexico during the fall, traveling as far as 1,840 km, and do not return to Texas caves in the Edwards Plateau until the spring (Glass 1982). The maximum documented migration rate was 32 km/day (Villa and Cockrum 1962). Cold weather appears to be an important factor spurring bat movement in the fall (Constantine 1967; Svoboda and Choate 1987). Brazilian free-tailed bats change roosts frequently before and after the maternity season. In the spring, population sizes fluctuate greatly in caves in Kansas (Twente 1956), and Davis cave in South Central Texas appears to be a staging area in spring for bats going north to caves in Oklahoma (Short *et al.* 1960). In the fall, populations shift from caves to nearby bridges (Horn and Kunz 2008).

The considerable variation in migration strategies found in Brazilian free-tailed bats may be analogous to the well-studied populations of Blackcaps (*Sylvia atricapilla*) found across Europe and Africa which show wide variations in migratory strategies with very little population structure (Perez-Tris *et al.* 2004).

Migration in Old World Fruit bats

In general, even less is known about migration of Old World fruit bats than for microchiropteran insectivores, and there are undoubtedly many migratory bats in tropical areas that are as yet unstudied (Fleming and Eby 2003). Most documented migration by fruit bats is regional rather than long distance, not directional, and tracks ephemeral food resources (Fleming and Eby 2003). A notable exception to this is the straw-colored fruit bat (*Eidolon helvum*). At least one population of these large bats leaves their African savanna habitat during the dry season and flies up to 2,518 km (Richter and Cumming 2008) to take advantage of large fruiting events (Richter and Cumming 2006). Between five to 10 million *E. helvum* spend October through December at Kasanka National Park in north-central Zambia, arriving as fruit begins to ripen and leaving as fruit production slows (Richter and Cumming 2006). It is unclear whether this number of bats and their foraging pressure is sustainable, as the areas with high levels of bat visitation are degraded, resulting in higher tree mortality and fire risk (Byng *et al.* 2010). Richter and Cumming (2008) tracked four male *E. helvum* with

satellite transmitters from Kasanka back to the Democratic Republic of Congo (DRC). During migration, bats moved an average of 90 km/day, and traveled up to 2,518 km in 149 days. Thomas (1983) suggests this movement is to avoid competition for fruit resources. While fruit is available year-round in DRC, the volume of fruit available around Kasanka evidently supports the long-distance effort.

Other examples of wide-ranging movements of fruit bats are less obviously migratory. A number of *Pteropus* species have been studied due to concerns that the bats serve as reservoirs for viral pathogens; at least three *Pteropus* species are known to carry Hendra or Nipah viruses. Radiotracked *P. vampyrus* travelled across political borders in Southeast Asia (Epstein *et al.* 2009), including Thailand, Sumatra, Malaysia, and Indonesia. The largest distance recorded for an individual was 363.4 km and one bat covered 130 km in 2 hours while foraging (Epstein *et al.* 2009). In another case, a *P. alecto* traveled over 3000 km moving in multiple directions (Breed *et al.* 2010).

Future directions in bat migration research

Our knowledge of migration in bats has been limited by available technology (Griffin 1970) and, as new technologies are being applied to this work, we are on the brink of learning much (Bridge *et al.* 2011; Cryan and Diehl 2009; Holland and Wikelski 2009).

Satellite tracking offers the best chance for long-distance tracking of individuals (Wikelski *et al.* 2007), but current satellite transmitters are too large for use on most bats due to limitations to the package weights that bats can carry without disrupting normal behaviors (Aldridge and Brigham 1988). However, exciting results are coming in from tracking large bats using satellite tags and GPS studies (Richter and Cumming 2008; Tidemann and Nelson 2004). Smith *et al.* (2011) tested various designs of satellite tracking technologies on *Pteropus* bats and found that optimal design was species- and ecology-specific with no single best solution. Solar powered transmitters only work for bats that roost higher in canopy so that batteries can re-charge during the day. In addition, current limits in technology mean that most tests are only on larger males that are able to carry heavier payloads.

Stable isotopes provide another tool for inferring movements of individual bats over long distances. Animals incorporate stable hydrogen isotopes (δD) into tissues and fur from water, and by matching isotope values from tissue samples with known values from water sources across a geographical or altitudinal gradient, it is possible to determine where the animal lived when those tissues were formed. Stable hydrogen isotope (δD) values from the hair of bats from

captures or museum collections have been used to identify movement patterns for North American tree bats (Britzke *et al.* 2009; Cryan *et al.* 2004). Fraser *et al.* (2012) showed that contrary to previous assumptions, male tri-colored bats (*Perimyotis subflavus*) tend to migrate in north-south directions like other tree-roosting hoary or silver-haired bats rather than like regional migrants, which may be due to a preference for warmer wintering sites farther south. All studies concluded that stable isotope technology is promising but more work is needed to understand the underlying hydrogen isotope gradients in water supplies at a small enough granularity to provide more meaningful spatial resolution. It is also crucial to understand molt patterns, because bats species vary in annual molt cycles and this will affect δD values. Fraser *et al.* (2010) underscored the limitations of this technology to study altitudinal migration in tropical areas without a better understanding of patterns of molting. However, a European study used δD values from hair from known sedentary bat species to avoid the molt-timing problem (Popa-Lisseanu *et al.* 2012). When combined with $\delta^{13}C$ and $\delta^{15}N$ values, predicted locations of known bat samples were significantly more accurate, suggesting this approach could be useful in determining breeding origins of bats.

Advances in radar technologies allow tracking the movements of individuals and groups of individuals, and possibly to distinguish among taxa (Ahlen *et al.* 2009; Chilson *et al.* 2011; Gauthreaux *et al.* 2008; Horn and Kunz 2008 but see Kunz *et al.* 2007a). Bruderer and Popa-Lisseanu (2005) compared video and radar data to differentiate small, medium, and large bats from migrating birds, although distinguishing among similar-sized bats (eg *Nyctalus noctula* and *Eptesicus serotinus*) required analysis of additional behavioral or ecological features. Their data also showed that during migration, flight speeds for *N. noctula* and *E. serotinus* were higher than expected. Study-specific radar installations are not necessarily required to apply this technology to broader questions of bat migration. The newly developed National Mosaic and multi-sensor Quantitative Precipitation Estimation system (NMQ) web portal offers public access to NEXRAD historical data that will enable tracking of migrants across North America (Chilson *et al.* 2011), but much work needs to be done to standardize the data sets for biological use.

A number of papers have presented promising and exciting potential areas for bat migration research. Hedenstrom's (2009) work on theory of bat migration offers predictions on timing and speed of migration, and where and when bats feed. McGuire and Guglielmo (2009) and Guglielmo (2010) compare the physiology of bird and bat migration and list research questions for future study, some of which they have begun to explore (McGuire 2012). Popa-Lisseanu and Voigt (2009) point out research opportunities involving migratory behavior, for example determining if bats migrate together (Ahlen *et al.* 2009) and how young bats learn their way. Holland (2007) outlines potential future directions for

research on navigation in bats. We believe the following areas will be at the forefront of migration research on bats in the next decade: 1) placing bats in the theoretical context of migration, 2) understanding the physiology of energy storage and use during migration, 3) exploring links between seasonal and spatial changes in food availability, the timing of migration events, and the use of stopover locations in bats, 4) documenting long-distance movements of individual bats across international boundaries and establishing connectivity of their populations through use of satellite technology, and 5) learning more about individual and group movements and assessing population sizes and trajectories using information from radar networks. The continued growth of wind power and its impact on bat populations as well as effects of climate change on the movements of bats, their prey, and the pathogens that they vector all suggest that migration in bats will be an increasingly important focus of research.

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CHAPTER II
AN INTEGRATIVE STUDY OF WEATHER-DRIVEN DYNAMICS IN
A DUAL-MIGRANT SYSTEM

Abstract

Animal migrations generate large spatial and temporal fluctuations in biomass that provide a resource base for many predator-prey interactions. These interactions are often driven by continent-scale weather patterns and are difficult to study. We tracked migrations of five species of agricultural pest noctuid moths over the 2010-2012 fall seasons as they traveled past a large colony of migratory Brazilian free-tailed bats (*Tadarida brasiliensis*) in Texas. Increases in moth abundance and mass of bats, and reductions in the duration of bat activity outside of the cave were significantly correlated with passage of cold fronts over the study area and resulting increases in northerly wind. Moth responses to weather patterns varied among species and seasons, but overall abundances were low in late summer and spiked after one or more cold front passages in September and October. Changes in bat mass and behavior were not directly linked to passage of migratory moths. Instead, those changes may be evidence of bat migration, as cave use transitioned from summer maternity roost to fall migratory stopover sites. Weather-driven migration is at considerable risk from climate change, and bat and moth responses to that change may have significant impacts on agricultural systems and bat ecosystem services.

Introduction

Animal migrations represent huge pulses of resources across landscape-scale areas (Dingle 1996, Chapman et al. 2003), and the scope and magnitude of migrations can be expected to significantly impact ecosystem dynamics (Yang et al. 2008). Because most migrants are fueled by fat reserves (Bairlein 2002, Hein et al. 2012), they should be valuable prey. However, migration events are often driven by weather (Shamoun-Baranes et al. 2010) and thus difficult for predators to predict. Game theory suggests that non-aggressive generalist predators should be best able to take advantage of unpredictable resources (Overington et al. 2008); i.e. social predators are able to work together to locate the resources in space and time, and generalists can modify their behaviors to respond to a variety of prey. Patterns of movement and response playing out on large scales are important to understand, yet are rarely studied from an integrative perspective (Bowlín et al. 2010).

High-altitude nocturnal insect migrations (Chapman et al. 2011) are an attractive resource for predators (Rankin and Burchsted 1992). Continent-spanning migrations have been documented in Australia, East Asia, Africa, Europe, and North America (Drake and Gatehouse 1995). Some of the most destructive

agricultural insect pests are migratory moths in the family Noctuidae (Mitchell et al. 2006). These moths are generalists, fecund, and migrate widely to avoid temperature extremes and drought and to track resources. Some noctuids are obligate migrants in temperate areas and use migration to avoid temperature extremes or to track suitable host plants. Others are facultative migrants, able to either migrate when conditions are favorable, or to enter diapause, a genetically programmed period of quiescence (Triplehorn and Johnson 2005), to wait for more favorable climate conditions and host plants. Research on migratory pest movement has been biased toward spring when crops are most vulnerable to damage (Leskinen et al. 2011). While much is thus known about northward movement of noctuid moths into North America in spring (Domino et al. 1983, Showers et al. 1989, Fitt 1989, Beerwinkle et al. 1994, Pair et al. 1995), until recently there was doubt that these insects underwent a return migration in fall (Johnson 1987, McNeil 1987, Pair et al. 1987, Gould et al. 2002), and little is known about the mechanisms influencing this behavior (Showers et al. 1993).

While many predators are likely to take advantage of migratory insects after they arrive, few would be able to locate and capture them *en route*. There is evidence that bats share foraging information (Wilkinson 1992, Ratcliffe and ter Hofstede 2005, Gillam 2007, Dechmann 2009) but few of these social species are insectivores and capable of high-altitude flight. Brazilian free-tailed bats (*Tadarida brasiliensis*) are generalist predators (Lee and McCracken 2005) that forage at high altitudes (Williams et al. 1973, McCracken et al. 2008). They roost in large colonies in the direct paths of migratory moth routes, can use unpredictable resources (Lee and McCracken 2005, McCracken et al. 2008; 2012), and are known to eavesdrop on conspecifics to find prey (Gillam 2007). Brazilian free-tailed bats are themselves long-distance migrants (Krauel and McCracken 2013) and must gain mass in the fall (Pagels 1975, O'Shea 1976) to fuel their own migration.

Many animal migrations are influenced by climate and weather (Shamoun-Baranes et al. 2010), especially insects (Drake and Farrow 1988). In North America, northward migration in spring is aided by typical patterns of low pressure in the Northern Plains and high pressure off the eastern coast, resulting in an anti-clockwise wind from the Gulf of Mexico moving north into the agricultural regions of the Great Plains (Johnson 1995). This pattern is periodically reversed in the fall, with barometric pressure gradients generating waves of cold fronts moving south from the Plains toward the southern US (Johnson 1995). Cold front passage is generally followed by a few days of northerly wind with higher than normal speed (Showers et al. 1993).

This study examines a dual-migrant system in southern Texas to investigate relationships between weather patterns, fluctuations in migratory noctuid moth abundances, and migration-related changes in behavior and resource acquisition of Brazilian free-tailed bats. We hypothesize that changes in noctuid moth

numbers are linked to changes in regional (cold fronts) and local (wind) meteorological patterns, and that bat flight activity and changes in body mass are linked to the same weather patterns. We predict that 1) local abundance of noctuid moths increases with frontal passages and favorable northerly wind, 2) bats gain mass with frontal passages, and 3) bats are active for shorter periods when resources are more available.

Material and Methods

Study area

This study took place at Frio Cave, Uvalde County, Texas (29° 26' 4.488", -99° 41' 5.028"), and adjacent agricultural areas. This cave is approximately 120 km west of San Antonio on private ranchland on the southern edge of the Edwards Plateau and hosts one of the largest known cave colonies of Brazilian free-tailed bats, with 1-2 million bats each summer (Betke et al. 2008). The area south of the cave consists of ranchland and farmland known as the Winter Garden. Primary summer crops include corn, cotton, soybean and sorghum; in the fall, some fields are used for sweet corn or late cotton crops, while others are used for vegetables or are left fallow.

Insect Monitoring

Insect samples were collected during three field seasons: between September 8 and October 21, 2010; September 7 and November 15, 2011; and August 25 through November 13, 2012. Insect traps were deployed at three agricultural field sites near Uvalde, Texas and one additional control site was located on a nearby livestock ranch that lacked nearby crops that might pests. These insect sampling sites ranged southeast from the cave along an 8 km transect. Three additional replicates were deployed at College Station, Texas, approximately 400 km to the northeast of Frio Cave. We deployed pheromone traps spaced approximately 50 m apart at each replicate site to attract adult male moths, each baited for a specific noctuid pest: corn earworm (*Helicoverpa zea*), fall armyworm (*Spodoptera frugiperda*), and cabbage looper (*Trichoplusia ni*).

Corn earworm traps were wire cone traps baited with Trece (Adair, OK., USA) lure TR-CEW 3138; fall armyworm and cabbage looper traps were universal plastic bucket traps baited with Scentry 2 (Billings, MT., USA) component lure SC-FAW L105B and Trece lure TR-CL 3119, respectively. In 2012, additional wire cone traps for black cutworm (*Agrotis ipsilon*) and true armyworm (*Pseudaletia unipuncta*), baited with Trece lures TR-BCW 3141 and TR-AMW 3205 respectively, were added at each replicate. Lures were replaced within recommended expiration periods, usually weekly. All insect traps were checked

daily and insects were frozen for later analysis. In 2010 and 2011, a VantagePro weather station (Davis Instruments, Hayward, CA) near one of the insect field sites recorded hourly temperature, humidity, rainfall, barometric pressure, and other relevant data. Weather-related information during 2012 was taken from the station at the Garner Field airport, Uvalde, except for readings for barometric pressure, which came from the nearby airport at Hondo, TX.

Acoustic Monitoring

We deployed Anabat II detectors (Titley Scientific, Columbia, MO, USA) approximately 25 m east and 30 m west of Frio Cave entrances to record bat activity around the cave in 2011 and 2012. Nightly foraging activity began with the main colony emergence, which was easily identified by our detectors. Acoustic signals at the cave entrances slowed after the main emergence but were continuous throughout the night. We considered the end of nightly activity time to be the end of last regular pulse of bats returning to the cave. Recordings of stragglers returning to the cave were discarded as not being representative of colony activity as a whole.

Bat Data Collection

Approximately every second day we sampled bats returning to Frio Cave after foraging, following Lee and McCracken (2002, 2005). Twenty-five bats were caught 1-2 hours before dawn using padded hand nets or mist nets, individually placed in clean cloth bags, and kept in a warm, dark, quiet area. After three hours, we recorded standardized measurements of mass, sex and reproductive status, age and forearm length, and released the bats into the cave. Methods complied with approved University of Tennessee animal care and use protocol no. 1947.

Cold Front Analysis

Moth migration events are likely initiated by cold front passage in areas where adult moths are sensitive to relevant cues such as changes in day length and air temperature, and possibly wind direction (Muller and Tucker 1986). In the North American Great Plains region, cold fronts often move from Kansas southward into Texas, but may dissipate at ground level before passing entirely through the study area. However, high-velocity northerly wind may continue despite the lack of a well-defined local frontal passage, and may carry migrating insects (J. Westbrook, pers. comm.). Previous studies document large numbers of insects moving southward in northerly winds directly following the leading edge of cold front passage in the Central Texas area (Beerwinkle et al. 1994). In the current

study, passage of large-scale cold fronts over the study area was identified by visual analysis of frontal patterns on Daily Surface Weather charts (Daily Surface Weather Map 2012) following Lee et al. (2012).

Data analysis

We modeled corn earworm abundance in analysis using average numbers of moths captured across three agricultural site replicates. Fall armyworm numbers in 2011 and 2012 also were averages; all other moth numbers were too low to use average values after correction for temporal autocorrelation, so we modeled moth abundance using total numbers of moths in all replicated pheromone traps. Meteorological predictor variables were daily values for nightly hours of northerly wind, low air temperature, low dew point, and low barometric pressure. We represented passage of cold fronts at Uvalde as factors coded as 1 for each day of frontal passage and 0 otherwise. Since moths may need northerly winds to move southward in the fall, we calculated the number of hours per night, based on local civil twilight, with wind from any northerly direction ($< 90^\circ$ or $> 270^\circ$). Moth abundance numbers, meteorological data, and length of bat flight activity had significant temporal autocorrelation. We removed autocorrelation and seasonal trends by taking the first difference of each daily value (DeLurgio 1998). Thus, values represent the change in each variable from the previous day. To identify which factors best explained variation in moth abundance, we computed cross-correlations (DeLurgio 1998) between daily numbers of moths caught in pheromone traps for each moth species and meteorological variables. Cross-correlations were considered significant when they exceeded 2 divided by the square root of the number of observations (DeLurgio 1998). Because relationships between moth numbers and predictor variables are likely to vary over time, we calculated cross-correlations for lags of up to two days. It was not appropriate to use linear regression to model moth abundances because the data contained significant outliers, and no other statistical model produced residuals with normal distributions.

We used multiple linear regression to answer the question of which factors best explain variation in duration of bat flight activity at the cave in 2011 and 2012. When duration of bat flight activity was significantly correlated with biologically meaningful lags or leads in a variable, we included variables offset by that lag or lead in the initial regression model (Legendre and Legendre 2012). We removed variables that were less important in the full model to identify the model with the highest adjusted r^2 value as the best for each response variable. Because model parameters can contribute substantially to the overall model r^2 even if they are not significant in themselves, we report the relative importance for each variable in the best models (R package relaimpo, Grömping 2006). Relative

importance describes the amount of variation in a response variable that is produced by a particular predictor variable.

To determine the relationship between changes in bat mass and cold front passages, we compiled a set of pairs of bat mass values from consecutive sampling days over all three years. We ran 5,000 one-tailed paired t-tests on randomly selected pairs to construct a boot-strapped distribution of all next-sampling-day changes in bat mass. We then compared paired t-test values of changes in mass on nearest days of frontal passage to that overall distribution. Female mass was consistently greater than that of males, so we analyzed males and females separately. All tests were run using R (v 3.0.2, 2013-09-25, Core Team 2013).

Results

We caught 35,509 moths in pheromone traps at Uvalde during the three field seasons (195 days total), 84% of which were corn earworms, and 28,145 moths in pheromone traps at College Station, of which 86.5% were corn earworms. Proportions of other species varied between years (Table 1). We caught 2,318 *Tadarida brasiliensis* bats during this same time, of which 64% were female and 36% male.

Weather varied between years; 2010 was a very wet year until October (National Weather Service) but had few cold front events in the fall. This was followed by extreme drought in 2011 despite much more frequent cold fronts, and that drought worsened in 2012. The number of nightly hours of northerly wind was positively correlated with frontal passage in all three years (Table 2). Because temperature, dew point, and barometric pressure were highly correlated with cold front passage and northerly wind, for simplicity we excluded those variables from analysis of moth abundances.

Moth abundances at pheromone traps significantly increased the day after cold front passages in all years and at both sites. Detailed responses of moths to weather by species, site, and year are listed in Table 3 and shown in Figure 2.1a-c; here we briefly describe patterns therein. Corn earworm numbers did not show any significant patterns in 2010, but in 2011 and 2012 responded primarily to cold front passage, with numbers increasing the day after frontal passage. Fall armyworms showed a less uniform response, with a strong correlation between increase in numbers and nights with higher amounts of northerly wind at Uvalde in 2010, and at College Station in 2011. Compared to other species, cabbage looper response was slightly delayed; numbers increased two days after frontal passage overall in Uvalde and there was no significant pattern at College Station in 2010 and 2011. In 2012, cabbage looper response was most closely associated with increased northerly wind the previous night at both sites.

Data was only available for true armyworm and black cutworm in 2012, when both species numbers increased the day after increasing northerly winds.

Moth numbers at College Station and Uvalde sites were temporally related (Table 2.4). When years are pooled, fall armyworm numbers increased a day earlier at College Station than at Uvalde but the pattern was reversed for cabbage looper, which increased a day earlier at Uvalde than at College Station. In 2010, corn earworm numbers increased at College station two days before rising at Uvalde, and in 2011 there was a strong correlation with fall armyworm numbers increasing at College Station the day before increasing at Uvalde. Black cutworm numbers increased two days later at College Station than at Uvalde in 2012. There was no significant relationship between sites for true armyworm.

Linear regression models explained 34% of variation in duration of bat flight activity at Frio Cave (Table 2.4, Figure 2.2) in 2011, 33% in 2012, and 25% with both years combined. In no models did the abundances of any moth species significantly explain duration of bat activity. In 2011, duration of bat flight activity increased as temperature lows decreased on the same and previous day. In 2012, bat flight duration decreased on the day of frontal passage and following increasing northerly wind and low temperature. In the dataset pooled over both years, the best model showed duration of bat flight increasing the day of cold front passage, and the day after increasing temperature and nightly hours of northerly wind.

Female bats gained mass in all three years (Fig. 2.3), and the mass gains were significant in 2011 ($r^2 = .60$, $P < .001$) and 2012 ($r^2 = .33$, $P < .001$). Variability of female mass increased as the season progressed, based on standard deviation of mass in 2010 ($r^2 = .38$, $P = .002$), 2011 ($r^2 = .31$, $P < .001$), and 2012 ($r^2 = .41$, $P < .001$). Males also gained mass in 2011 ($r^2 = .61$, $P < .001$) and 2012 ($r^2 = .12$, $P = .03$), but not in 2010. Male masses were less variable than those of females, with a small but significant increase in variability only in 2011 ($r^2 = .17$, $P = .02$). Both male and female bat mass increased more in association with cold front passages than on other consecutive sampling days (males: $t = -2.092$, $P = .03$ and females: $t = -3.56$, $P = .003$).

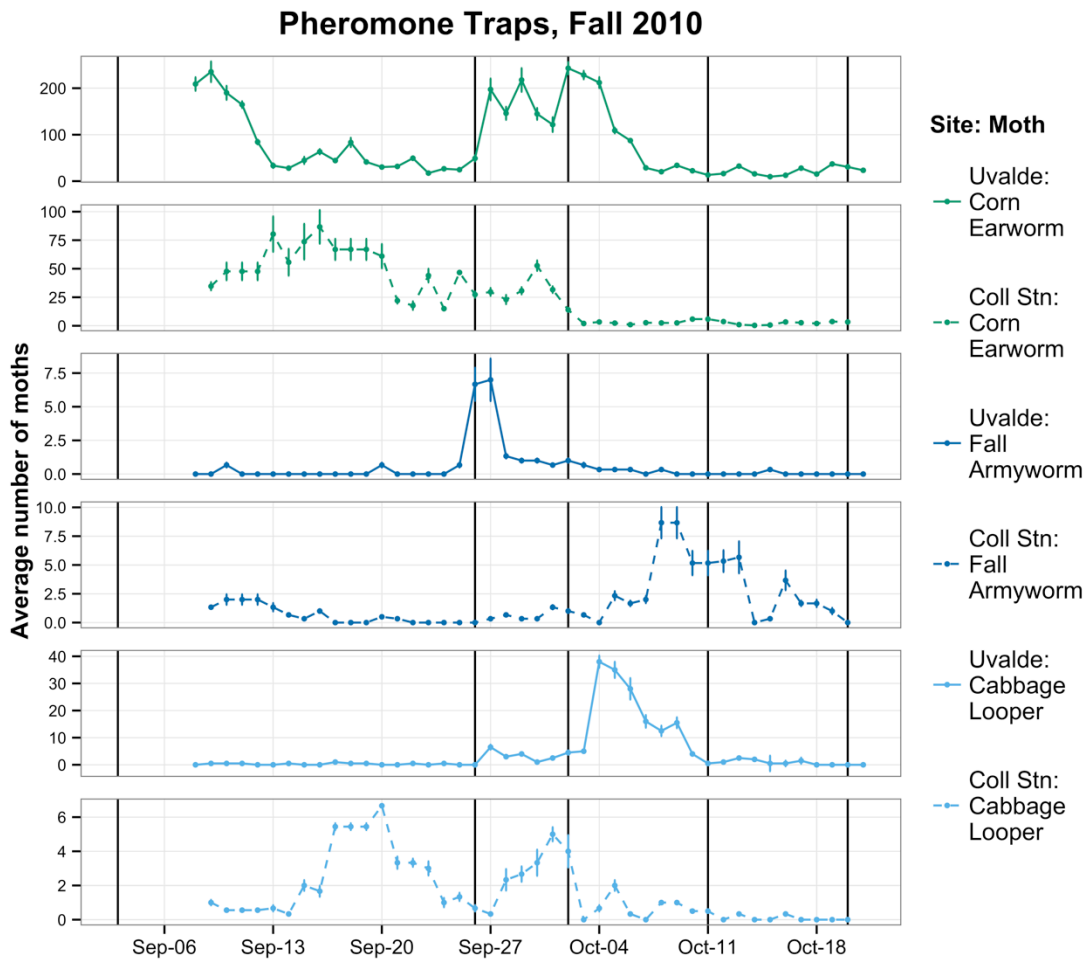


Figure 2.1a. Pheromone trap results, 2010.

Average moth captures by species at pheromone traps in 2010. Solid lines represent Uvalde captures, and dashed lines represent moths caught at College Station. Note that the scale of the vertical axes varies significantly between species and years. Error bars represent standard errors for each moth species, site, and date. Vertical black lines represent day of cold front passage at Uvalde, TX.

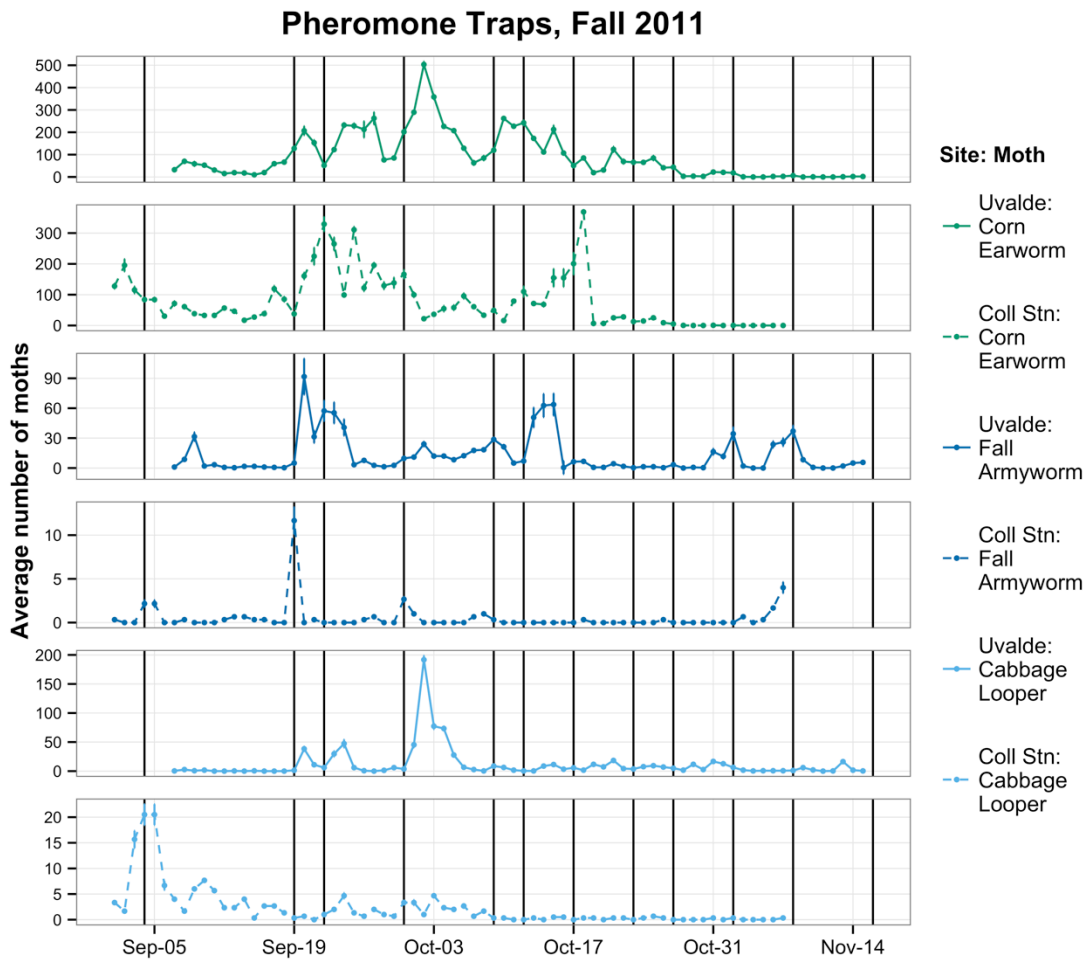


Figure 2.1b. Pheromone trap results, 2011.

Average moth captures by species at pheromone traps in 2011. Solid lines represent Uvalde captures, and dashed lines represent moths caught at College Station. Note that the scale of the vertical axes varies significantly between species and years. Error bars represent standard errors for each moth species, site, and date. Vertical black lines represent day of cold front passage at Uvalde, TX.

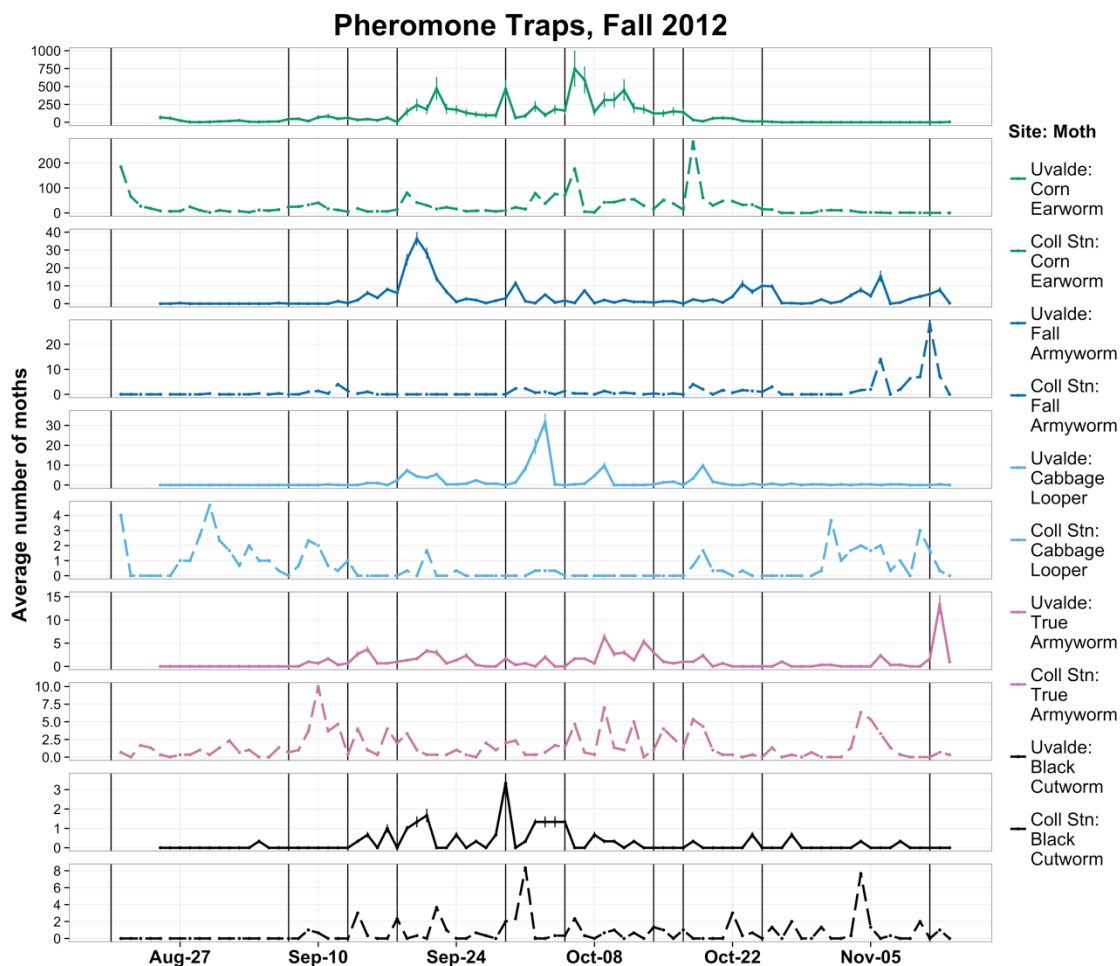


Figure 2.1c. Pheromone trap results, 2012.

Average moth captures by species at pheromone traps in 2012. Solid lines represent Uvalde captures, and dashed lines represent moths caught at College Station. Note that the scale of the vertical axes varies significantly between species and years. Error bars represent standard errors for each moth species, site, and date. Vertical black lines represent day of cold front passage at Uvalde, TX.

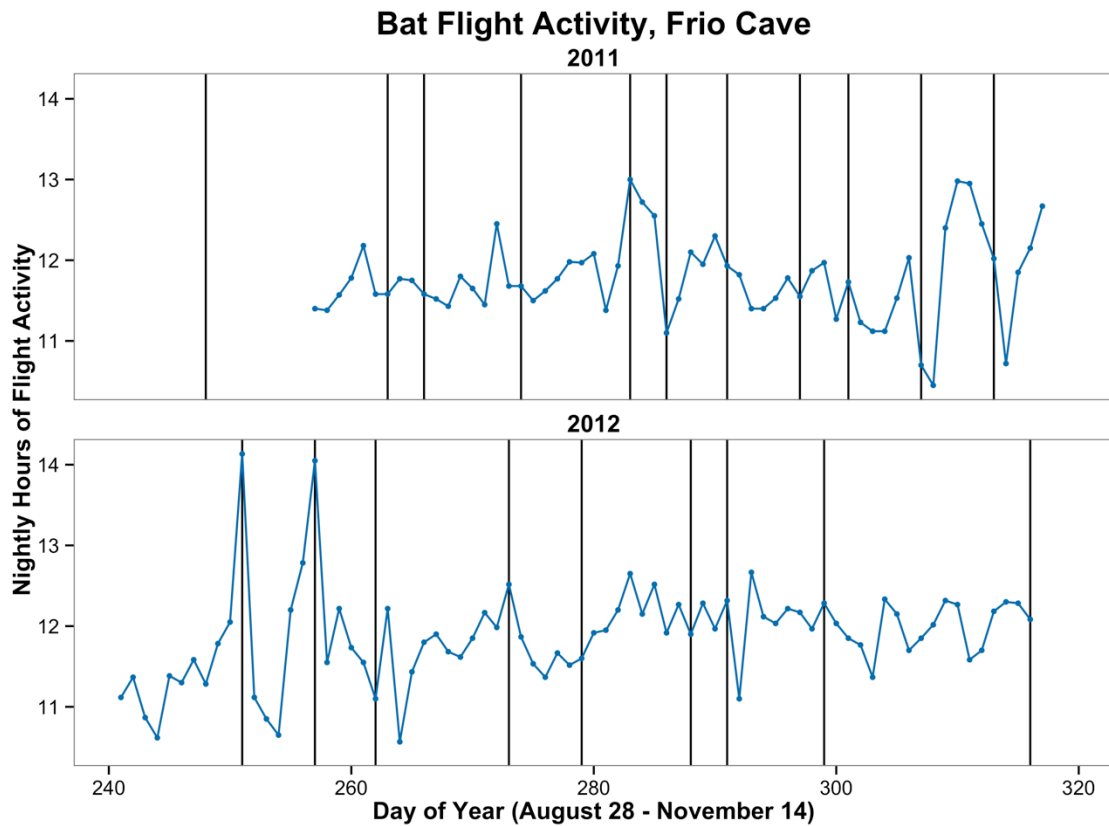


Figure 2.2. Bat flight activity.

Length of time bats were actively flying outside of Frio Cave, Uvalde Co., TX during the 2011 (upper) and 2012 (lower) fall season, in hours, as measured by acoustic detectors placed adjacent to cave entrances. See text for details. Vertical black lines represent day of cold front passage at Uvalde, TX.

Frio Cave bat mass, Fall 2010-2012

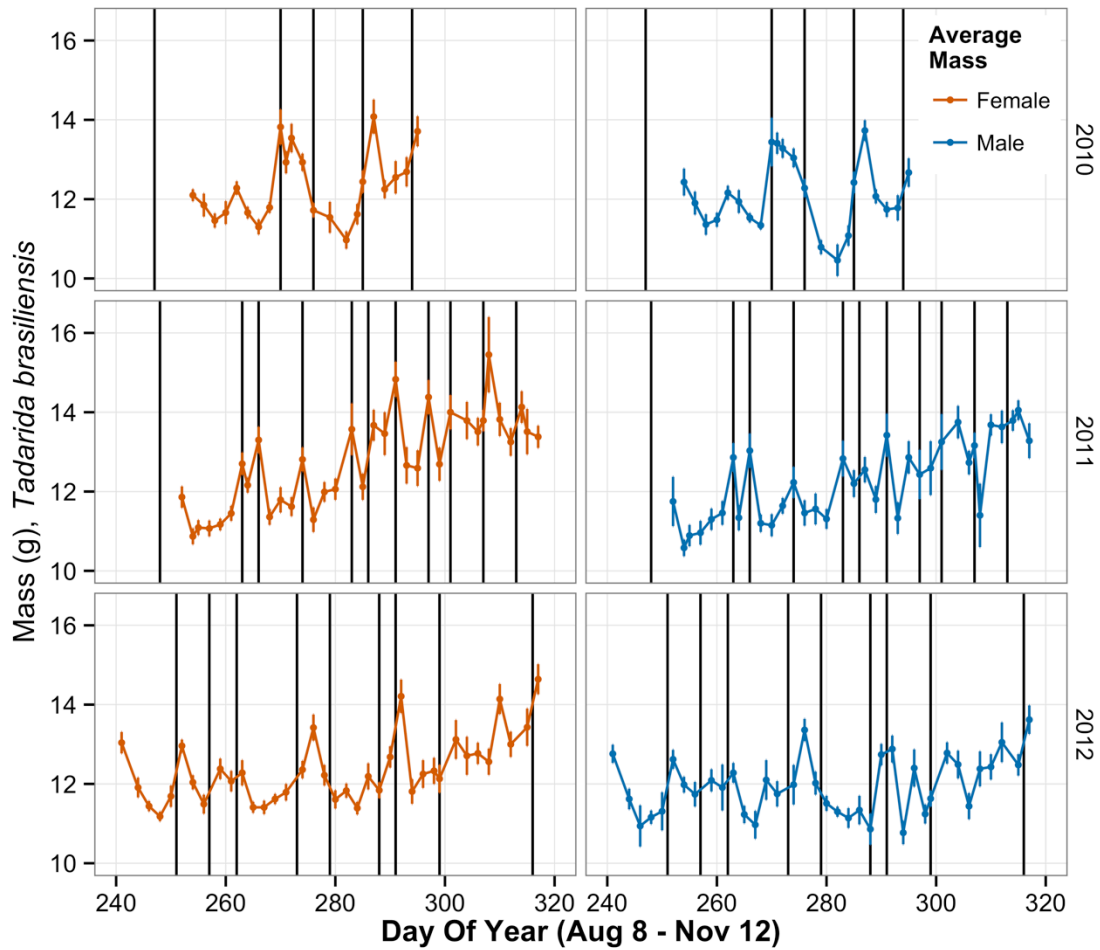


Figure 2.3. Bat mass.

Average bat mass (*Tadarida brasiliensis*) for males and females caught at Frio Cave, Uvalde Co., TX in 2010 (top), 2011 (middle), and 2012 (bottom). Error bars represent standard errors. Vertical black lines represent day of cold front passage at Uvalde, TX.

Table 2.1. Total moths caught in traps.

Total number of moths caught in all pheromone trap replicates by moth species, year, and site (Uvalde and College Station, TX)

Moth	Year	Total Uvalde	Total College Stn.
Corn Earworm	2010	10,724	3,416
	2011	19,891	15,755
	2012	7,683	6,949
Fall Armyworm	2010	69	207
	2011	2,944	100
	2012	899	319
Cabbage Looper	2010	612	202
	2011	2,581	452
	2012	468	164
True Armyworm	2012	299	385
Black Cutworm	2012	63	196

Table 2.2. Cross correlations between cold fronts and met. variables.

Significant cross-correlations between passage of cold fronts at Uvalde, TX and meteorological variables.

	Year	2 days prior	Previous day	Same day	Day after	2 days after
Cold Front	2010			W +0.33		
	2011	T +0.25 D +0.31	W +0.45	D -0.34	W -0.35 D -0.37 B +0.45	T -0.25
	2012		B -0.27		W +0.41 D -0.39 B +0.41 T -0.39	T -0.27
	All		W +0.21 B -0.20	D -0.16	D -0.32 B +0.39 T -0.30	T -0.27
Wind	2010		D +0.34 T +0.31		B +0.46 T -0.31	
	2011		D +0.40 T +0.38	B -0.50	D -0.38 B +0.35	B +0.36 T -0.38
	2012		D +0.25 B -0.33	D -0.31	D -0.28 B +0.29	T -0.38
	All		D +0.30 T +0.25	D -0.33 B +0.29	D -0.29 B +0.33	T -0.25

W = hours of northerly wind at night, D = daily low dew point, B = daily low barometric pressure, T = daily low temperature. Data shows a significant and typical pattern of nightly hours of northerly wind rising and barometric pressure falling one day before frontal passage, and low dew point and low temperature falling for two days afterward. Barometric pressure rose the day after frontal passage in each year.

Table 2.3. Cross correlations between moth abundance and fronts.

Significant cross-correlations between moth abundance and weather variables.

Moth species	Year	Site	2 days prior	Previous day	Same day
CEW	2011	UV			W -0.26
		CS	F -0.37	F +0.26	
	2012	CS	F -0.37	F +0.40 W -0.25	W +0.29
	All	UV		F +0.17	
		CS All	F -0.32	F +0.29 F +0.20	
FAW	2010	UV	F -0.37		F +0.39 W +0.44
	2011	CS		F -0.26 W +0.36	F +0.29
	2012	UV		F +0.26	
	All	CS			F +0.27
		All		F +0.20	
CL	2010	UV	F +0.47		
	2011	UV	F +0.25		
	2012	UV		W +0.27	
		CS		W +0.26	
	All	UV All	F +0.20 F +0.23		
TAW	2012	UV	W -0.23	W +0.33	
		CS All		F +0.30 F +0.26 W +0.17	
BCW	2012	All		W +0.20	
All	All	UV		F +0.15	
		CS	F -0.30	F +0.20	W +0.19
		All		F +0.17	

Table 2.3. Continued

F = passage of cold fronts, W = hours of northerly wind at night, UV = Uvalde site, CS = College Station site. Moth species: CEW (corn earworm), FAW (fall armyworm), CL (cabbage looper), TAW (true armyworm), and BCW (black cutworm). Numbers represent the correlation between numbers of moths caught in pheromone traps and the value of key weather variables the same day, the day before, and two days prior. E.g., the number of all moths caught in all seasons at the Uvalde site was positively correlated ($r = 0.15$) with passage of a cold front the previous day.

Table 2.4. Cross correlations between moths in both sites.

Significant cross-correlations between moth abundances at Uvalde and at College Station sites.

Moth	Year	2 days prior	Previous day	Same day	Day after	2 days after
CEW	2010	+0.41				
	2011	-0.26				
	2012				-0.23	
	All	-0.16				
FAW	2011	-0.38	+0.70	-0.39		
	2012		+0.22	+0.37		
	All	-0.16	+0.27			
CL	2010			-0.35		
	2011				-0.31	
	All			-0.18	+0.21	
BCW	2012					+0.44

Moth species: CEW (corn earworm), FAW (fall armyworm), CL (cabbage looper), TAW (true armyworm), and BCW (black cutworm). Values correspond to the response of numbers at College Station with respect to changes in numbers at Uvalde. For example, corn earworm numbers at College Station increased two days earlier than they did at Uvalde in 2010. There were no significant inter-site correlations for true armyworm. Black cutworm and true armyworm were only trapped in 2012; all other moths were trapped over all 3 seasons.

Table 2.5. Models of bat flight activity.

Models best explaining variation in duration of bat flight activity near Frio Cave, Uvalde Co., Texas in 2011, 2012, and both years combined.

Year	Parameters	Coefficients \pm SE	Rel. Imp.	Model
2011	Temp B1 ***	-0.10 \pm .024	.204	Adj. r^2 = .34
	Temp *	0.05 \pm .02	.079	$F(4,55) = 8.59$
	Dew		.064	$P < .0001$
	Dew B1		.038	
2012	Wind B1 *	0.02 \pm .009	.112	Adj. r^2 = .33
	Wind		.100	$F(5,69) = 8.35$
	Temp B1 *	0.04 \pm .019	.074	$P < .0001$
	Front *	0.60 \pm .26	.055	
	Dew B1		.036	
All	Temp B1 ***	0.06 \pm .01	.162	Adj. r^2 = .25
	Wind B1 ***	0.02 \pm .005	.084	$F(3,131) = 15.97$
	Front **	0.40 \pm .15	.022	$P < .0001$

Temp = daily low temperature, Dew = daily low dew point, Wind = daily hours of northerly wind at night, Front = day of cold front passage at Uvalde, B1 = parameter represents the value of this variable the day before corresponding variation in duration of bat flight activity around Frio Cave, TX. In 2011, low dew point parameters were negatively correlated with duration of bat flight activity. In 2012, same-day wind was negatively correlated with duration of bat flight activity, and previous day low dew point was positively correlated with duration of bat flight activity.

*** $P < .001$.

** $P < .01$.

* $P < .05$.

Discussion

Weather, especially at a synoptic or continental level, is an important factor in migration for many animals, including birds (Able 1973, Richardson 1990), bats (Krauel and McCracken 2013), and insects (Muller and Rucker 1986, Showers et al. 1993). Weather patterns in this study showed a consistent trend of increasing northerly wind and decreasing temperature following local passage of cold fronts (Table 2.2), providing a mechanism for southward migration in fall (Showers et al. 1993, Johnson 1995).

Moths

Corn earworm, the largest and most numerous of our noctuid moth study species (Table 2.1), is a migrant in both spring and fall but is able to overwinter in the study area in diapause as well (Lopez et al. 1995, Westbrook and Lopez 2010). Fall armyworm is believed to be an obligate migrant due to an inability to diapause in cold climates (Johnson 1987, Nagoshi et al. 2009). Cabbage looper is also an obligate migrant and intolerant both of extreme cold and heat (Franklin et al. 2010). Most cabbage looper studies are from the Pacific coast region, and little is known about its migratory patterns in the study area.

In our study, most moth species showed a pattern of low numbers in late summer followed by a sudden increase on or shortly after cold front passage. Both cabbage looper and fall armyworm numbers were lower in 2010 than later years, which may have been due to an unusually wet spring (King 1966, Pair and Westbrook 1995). As in earlier studies (McCracken et al. 2012), there was a dramatic increase in the availability of corn earworm in mid-Sept, followed by a decline after the month's end (Figure 1a-c). In general, fall armyworm and cabbage looper showed activity over a longer period and extending later into the season than did corn earworm (Figure 1a-c). All moth species showed significant positive correlations with frontal passage or northerly wind, although the exact response varied among years and species. In particular, cabbage looper showed a slightly slower response to frontal passages, although it is unclear whether this is due to delayed arrival at the trap site, or delayed attraction to the traps themselves. The pattern was surprisingly weak for corn earworm in 2010, but this may be because traps were set up after the first suspected migration-related cold front passed through the study area. The College Station sites are 400 km northeast of the Uvalde sites, and moths are thought to migrate generally from northeast to southwest in the fall (Showers et al. 1997), which would be supported by arrival at College Station earlier than at Uvalde. Fall armyworm moths did arrive one day earlier at College Station than at Uvalde, but for other species there was not such a clear trend. In 2010, corn earworm moths arrived two days earlier at College Station than Uvalde, but in

other years there was not a positive relationship, and cabbage looper numbers increased a day earlier at Uvalde than at College Station overall. Data are available for black cutworm in 2012 only, but moths arrived at Uvalde two days earlier than at College Station.

Our study provides evidence that all five noctuid moth species responded significantly to cold-front-related favorable weather patterns. These results support earlier work showing that noctuid moths migrate with cold fronts in the fall. Beerwinkle et al. (1994) observed large numbers of insects moving south in northerly winds after a cold front in the study area. Pair et al. (1987) reported a peak of migratory fall armyworm and corn earworm in Brownsville, TX 1-3 days after cold front passage, in an area without host plants. Showers et al. (1993) dyed black cutworm and released them in Iowa when favorable northerly winds were expected; eight nights later dyed moths were captured at College Station, TX, and one individual was recaptured in Brownsville, TX.

While the provenance of moths caught in our pheromone traps is unknown, local corn earworm in Texas enter diapause in mid-September (Lopez and Hartstack 1985, Fitt 1989), and any increase in capture numbers likely represents migrants. Records from pheromone traps in potential migratory source locations (Fleischer et al. 2007) support this assertion. In all three years, cold front passages link the end of moth activity north of Texas to spikes in moth numbers in Uvalde. Large numbers of corn earworm were caught in traps at Manhattan, KS. in 2010 until Sept 24, when a cold front traveled south into northern Texas. (National Oceanic and Atmospheric Administration 2012). The front stalled there until Sept 27, when it moved south over Uvalde, with a resulting spike in corn earworm in our traps. Corn earworm appeared at Manhattan, KS. traps until Sept 25, 2011, and a frontal system moved through there on Sept 24 followed by high pressure. The front reached Uvalde on Sept 27, followed by the season's highest corn earworm numbers two days later. In 2012, a series of frontal passages brought peak fall armyworm numbers to Iowa on Sept 13, 17, and 19, and fall armyworm numbers increased at Uvalde on Sept 20.

Bat mass and activity

After producing and rearing pups, female Brazilian free-tailed bats are at their lowest fat levels in late August (Pagels 1975, O'Shea 1976, present study). High temperatures and parched vegetation likely contribute to reduced prey availability, as evidenced by the low numbers of moths in our pheromone traps at that time. Our study showed that both male and female bats gain mass as migratory moths move through the area during the fall season, and particularly that bats gained more mass in association with cold front passage than at other times. In addition to the pattern of mass gain, we documented higher proportions

overall of female than male bats, greater rates of mass gain in females than in males, and increasing mass variance over time in female bats.

Mass gain may be a direct result of consumption of migratory moths, although significant weight gain is likely to require more than a single night of foraging on high-fat-content prey. A more likely explanation for the observed patterns is the transition of Frio Cave from a maternity roost in summer into a migratory stopover (Krauel and McCracken 2013) in fall. Frio Cave is located on the southernmost edge of the Edwards plateau, a large karst area with many caves serving as roosts for free-tails and other bats (Short et al. 1960, Glass 1982). Migratory bats are known to take advantage of favorable wind associated with cold fronts (Cryan and Brown 2007). While we do not have data about bat population fluctuations at the cave during the study period, it was clear that numbers of bats returning to the cave increased dramatically on windy mornings after cold fronts. This is consistent with other reports showing that free-tailed bats change roosts with shifts in weather conditions in the fall (Twente 1956, Svoboda and Choate 1987, Scale and Wilkins 2007, Hristov et al. 2010). Little is known about control of migratory onset in bats, although in many taxa it is a combination of environmental cues and hormonally mediated thresholds (Ramenofsky and Wingfield 2007). Some bats are thought to undertake migration if they have accumulated sufficient fat reserves to complete the entire journey (McGuire et al. 2011). Although we could not track individual bats, our results may document the arrival of heavier bats moving south on favorable winds from more northerly roosts, which might explain the patterns seen in our data. That is, resident females would be smaller than incoming migrants, and as the number of migrants increases, variance in mass as well as average mass overall should increase in conjunction with waves of new arrivals with cold fronts.

Duration of bat activity around the cave increased after cold fronts and with rising temperatures and increasing northerly winds. Unlike previous studies conducted at Frio Cave earlier in the year (Lee and Kuo 2001, Reichard et al. 2009) which showed variation in both daily departure and return time, the bats in our study generally left the cave at sunset throughout the fall season, and differences in activity duration were primarily due to later returns at dawn. Previous studies also linked variation in activity duration to fluctuations in prey availability (Lee and Kuo 2001, Reichard et al. 2009). The difference in activity patterns, and the lack of association of activity time with fluctuations in moth abundance, suggest that foraging needs may not drive variation in duration of activity at the cave. As with mass gain, the activity patterns we documented may present further evidence of arrival of migrating bats. Some bats using the cave as a stopover site might arrive on favorable winds later than resident bats returning from local foraging. The result would be consistent with our observation of increased duration of activity on those dates. Anecdotally, this is also consistent with our general observation that on mornings with cold-front-associated northerly winds, many

bats entering the cave did not appear to anticipate our nets and were thus easier to catch.

Conclusions

This is the first integrative study of migratory predators and their migratory prey conducted across an entire season (Bowlin et al. 2010), and results confirm our hypothesis that the migratory process is primarily driven by weather (Shamoun-Baranes et al. 2010). Understanding this particular study system is important for many reasons. Migratory moths incur considerable economic damage to crops, and bats provide significant ecosystem services in control of those moths (Cleveland et al. 2006, Lopez-Hoffman et al. 2014). This overall system is driven by weather, which in turn now faces unpredictable perturbations due to climate change.

Brazilian free-tailed bats are one of the most widely distributed mammals in the western hemisphere (Wilkins 1989). The presence of migratory moths during a period of otherwise low resource availability may contribute substantially to the ability of free-tailed bats to undertake their own migrations. Because the moths are able to use native vegetation (Lopez et al. 1995), the advent of human agriculture may have augmented moth migration and perhaps driven a northward range extension by the bats (Russell et al. 2011), allowing bats to take advantage of the large cave system in the study area. These important free-tailed bat roost cave resources all along their migratory routes span international borders and thus represent a conservation challenge (Wiederholt et al. 2013, Berger et al. 2014).

Since weather is a primary factor in moth migration (Drake and Gatehouse 1995), and moth movements can reflect escapes from extremes of heat and cold (Showers 1997, Luo 2002), climate change is likely to have a significant impact on noctuid moth migration patterns (Parmesan 2001). Extreme wet or dry conditions can have a large effect on annual noctuid moth migration (Pair and Westbrook 1995, present study), and a period of extended drought is already documented in our study area. Changes in moth availability may have unpredictable effects on the bats. With fewer moths, bats may not gain enough mass to undertake their southward migrations, and thus may be forced to overwinter in the area. If milder winters enable moths to remain in the area (Bale and Hayward 2010), the overwintering bats could be an important control mechanism. However, overwintering corn earworm moths, the dominant moth in the study system, are likely to enter diapause to avoid heat and low host plant availability in late summer. They would thus be unavailable to the bats during this key period. Without a sufficient pulse of migrating moths, many bats may ultimately be forced to give up migration and remain in their wintering range,

resulting in a significant decrease in available pest control services in the study area.

Our results may be applicable to other systems involving bats adapted for high-altitude foraging near corridors used by migratory insects (Drake and Gatehouse 1995, Fenton and Griffin 1997, Leelapaibul et al. 2005). Such systems may have enabled the evolution of social foraging (Dechmann et al. 2010), or permitted bats to migrate by providing sources of high-quality nutrition when little else is available. Additionally, high-flying social bats found in areas supporting insect migrations may turn out to be migrants themselves. Integrative studies of animal migration are difficult, but provide important insights into complex relationships facing a variety of threats (Bowlin et al. 2010).

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CHAPTER III
BATS ADJUST FORAGING BEHAVIOR IN RESPONSE TO
MIGRATORY PREY

Abstract

Insect migrations represent large movements of resources across a landscape, and are likely to attract predators capable of detecting and catching them. Brazilian free-tailed bats (*Tadarida brasiliensis*) track resources in time and space and consume large numbers of migratory noctuid moths. During migration, moths fly at high altitudes in layers that exploit temperature, wind speed, and wind direction, resulting in prey concentrations that should be attractive to bats. While bats are known to feed on migratory moths, migration events have not been linked to shifts in foraging behavior of bats. We predicted that bats alter foraging patterns by flying at higher altitudes during moth migrations, and that they adjust their echolocation calls with altitude and numbers of moths. We recorded 1,104 Brazilian free-tailed bat passes at ground level and aloft at altitudes of ca. 100 and 200 m above ground level on 13 nights in fall 2012. During moth migration events, we found proportionally more bat activity at higher elevations than ground level. Altitude and numbers of moths explained 28% of all variation in echolocation call parameters describing duration and frequency of calls. Results support predictions that bats change foraging behavior in response to seasonal availability of migrating insect prey.

Introduction

Migratory movements of animals can result in rapid, dramatic shifts in the distribution of biomass across landscapes. Although often overlooked, insect migrations may involve more biomass and have greater impacts on ecosystem function than any other migratory system (Drake and Gatehouse 1995). For example, an estimated 3 billion insects pass over southern England on a typical summer day (Chapman et al. 2003). Most migratory moths increase fat reserves before migration, and should represent a rewarding resource for insectivorous predators (Cortes-Avizanda et al. 2011). However, these resources are usually ephemeral or otherwise difficult to predict. For example, moth migrations often occur at high altitudes (Drake and Gatehouse 1995) and vary greatly in time and trajectory even during a single season (Showers et al. 1989, Showers et al. 1993). To take advantage of migratory prey, a predator must detect migration events and, if migration events occur in places where prey are not normally available, predators will need to adjust foraging behaviors to find and capture them. The ability of predators to track and exploit migratory prey remains little studied, even as migrations are under considerable threat from climate change and the loss of habitat in breeding grounds, wintering grounds, or stopover sites (Parmesan and Bi 2001).

Bats are known to eat migratory insects (Kronwitter 1988, Lee and McCracken 2005, Leelapaibul et al. 2005). Brazilian free-tailed bats (*Tadarida brasiliensis*)

and their migratory noctuid moth prey (including the economically destructive corn earworm, *Helicoverpa zea*) are well studied (Wolf et al. 1990, Lee and McCracken 2005, McCracken et al. 2008, Reichard et al. 2009, McCracken et al. 2012), and provide an excellent system for examining interactions between highly mobile predators and migratory prey. In late summer, Brazilian free-tailed bats in Texas are stressed after raising their pups, with fat reserves at their lowest (Pagels 1975, O'Shea 1976). High temperatures and the lack of rainfall typical of late summer in the region also reduce the availability of moths (Lee & McCracken 2005). However, waves of lipid-rich (Rankin and Burchsted 1992) southward-bound migrating moths pass through the area in September and October as the moths take advantage of favorable northerly winds following cold fronts (Pair et al. 1987, Westbrook 2008). For example, in late September black cutworms (*Agrotis ipsilon*) can move 1900 km from Iowa to Texas in 8-14 nights (Showers et al. 1993). Thus, we expect that Brazilian free-tailed bats will exploit this resource, if possible.

Brazilian free-tailed bats have been documented flying (Williams et al. 1973) and foraging (Griffin and Thompson 1982) at high altitudes, including recorded feeding buzzes as high as 847 m above ground level (AGL) (McCracken et al. 2008, Gillam et al. 2009). These high altitude flights have been attributed to pursuit of migratory insect prey, and McCracken et al. (2008) documented a peak in bat activity at between 400-500 m AGL, coincident with altitudes of prevailing winds used by migratory insects to facilitate long distance movements. Further, fecal DNA analysis demonstrates spikes in corn earworm moth consumption coincident with both the spring and fall migrations of the moths (McCracken et al. 2012). Increased foraging activity at altitudes where moths migrate and increased moth consumption during periods of migration indicate that the bats take advantage of the insect migrations. However, no previous studies directly link high-altitude feeding and the behavioral responses of bats to insect migration events.

In addition to foraging where and when moths are migrating, bats might also change how they detect the moths. Echolocation calls of Brazilian free-tailed bats are diverse (Simmons et al. 1978, Gillam and McCracken 2007) and highly plastic (Ratcliffe et al. 2004, Gillam et al. 2010). An earlier study showed that temporal and frequency parameters of high-altitude foraging calls differed from those at ground level, with frequencies declining and call durations increasing at higher altitudes (Gillam et al. 2009). We speculated that flexibility in call structure might result in variation related to altitude or fluctuating prey density during moth migration events.

The objective of this study was to investigate the behavioral responses of Brazilian free-tailed bats to discrete moth migration events that occur in fall linked to advancing cold fronts. We present and test two hypotheses: 1) bats alter

foraging patterns to take advantage of increased abundance of migratory moths, and 2) bats shift echolocation call parameters with altitude and levels of moth abundance. We predict 1) there will be more foraging activity at higher altitudes during periods of higher migratory moth abundance than at other times, and 2) search phase echolocation call parameters will differ with altitude and levels of migratory moth abundance

Materials and methods

Study area

This study took place near Frio Cave, Uvalde County, Texas, and surrounding agricultural areas. Situated approximately 120 km west of San Antonio on private ranchland on the southern edge of the Edwards Plateau, Frio Cave (29° 26' 4.488", -99° 41' 5.028") hosts one of the largest known cave colonies of Brazilian free-tailed bats, with 1-2 million bats each summer (Betke et al. 2008). The area south of the cave consists of ranchland and farmland known as the Winter Garden. Primary summer crops include corn, cotton, soybean and sorghum; in the fall, some fields contain corn or late cotton crops, while others are used for vegetables or are left fallow.

Moth Monitoring

Moths were collected daily between August 25 and November 13, 2012 in pheromone traps deployed at three replicate agricultural field sites and one control site located on a nearby livestock ranch ca. 4 km from crops that might attract pests. Trapping sites ranged southeast from the cave along an eight km transect. Each site contained five pheromone traps, each trap set to attract adult male moths of one of five targeted noctuid pest species: corn earworm, fall armyworm (*Spodoptera frugiperda*), cabbage looper (*Trichoplusia ni*), black cutworm, and true armyworm (*Pseudaletia unipuncta*). In addition to pheromone traps, each site also included a blacklight trap (BioQuip, Model 2851L:22W) to monitor local insect emergences. Pheromone lures were replaced within recommended expiration periods, usually weekly, all insect traps were checked daily, and all moths were frozen for later analysis.

Cold Front Analysis

Cold fronts are events with patterns at both synoptic, or continent-wide, and local scales. Moth migration events are likely initiated by cold front passage in areas where adult moths are sensitive to relevant cues such as changes in day length and temperature, and possibly wind direction (Muller and Tucker 1986). In the North American Great Plains region, cold fronts often begin in middle latitude

areas such as Kansas and move southward into Texas, but may dissipate at ground level before passing all the way through the study area. However, high velocity northerly winds may continue at higher altitudes despite a lack of local frontal passage, and may carry migrating insects (J. Westbrook, pers. comm.). In the current study, passage of large-scale cold fronts over the study area was identified by visual analysis of frontal patterns on Daily Surface Weather charts (National Oceanic and Atmospheric Administration 2012) following Lee et al. (2012).

Migratory moth activity

For this study, we used spikes in numbers of moths caught in pheromone traps after local moths were in diapause as well as cold front passages as indicators of higher-altitude moth migration events. High numbers of noctuid moths are found throughout the study area during late spring and summer when forage crops are available. However, most of the local population of the most abundant moth, corn earworm, enters pupal diapause by mid-Sept in the study area (Lopez and Hartstack 1985). In this study, corn earworm represented 82% of all moths captured overall, and was found in low numbers until after a cold front on Sept 18.

Noctuid moths migrate with assistance of favorable winds (Chapman et al. 2008a, 2008b). Prevailing winds in the study area are typically from the south, and thus southward movement in the fall is likely to be restricted to periods of northerly winds associated with cold front passage (Sparks et al. 1986, Showers et al. 1993). Numbers of moths captured in pheromone traps in this study were significantly positively correlated with both cold front passage and nightly hours of northerly wind (this study, Chapter 2). Like many migratory insects, noctuid moths migrate at night at altitudes of 100m and higher (Westbrook 2008). In earlier years, noctuid moth captures in ground-level pheromone traps in the study area closely matched the radar documented mass movement of moths, with peak numbers moving at 200m AGL in the fall (Beerwinkle et al. 1995).

Because captures were a proxy for actual moth abundances during recording sessions, we considered moth migration as factor with two or three levels. For the two-level factor, we coded as 1 for moth migration events and 0 otherwise. We considered nights with total moth captures in the highest quartile (> 306 moths) occurring on the day of cold front passage or 1-2 days thereafter to represent moth migration events. For the three level factor, used in echolocation call analysis, we considered those moth migration event nights as high levels of activity. Nights with moth numbers in the first quartile (0 – 45) were considered to have low levels of moth activity, and remaining nights as having medium levels of moth activity.

Foraging activity

All acoustic recordings were made using SM2Bat detectors (Wildlife Acoustics Inc., Concord, MA, USA) at one of the moth trapping sites (29° 20' 3.552", -99° 42' 47.6274"), located 11 km SW of Frio Cave. We captured ground-level recordings at 1.5 m above the ground, and deployed two additional detectors at higher altitudes at the same site using a 3.3 m³ Skyhook Helikite (Allsopp Helikites Ltd, Hampshire, UK) (Verhoeven et al. 2009). The Helikite is a hybrid kite-balloon designed to enable lift in low winds and remain stable in high winds. We attached higher altitude detectors to spars taped to 300 kg test Dyneema line and deployed the Helikite using an electric winch (Goodwinch Ltd, Devon, UK). We let out at least 350 m of line in the late afternoon before bats began flying in the area, with the detectors attached at 100 m and 200 m below the Helikite. The two detectors deployed aloft were modified by removing external casing and switching to lightweight power supply. We then packaged those detectors in Styrofoam cylinders that were tapered so that the cylinders vaned into the wind with the microphones protected in the wind-shadow opposite the tapered end of the cylinder (McCracken et al. 2008). We turned on detectors at the time of initial deployment and turned them off as they were removed from the Helikite line at the end of a flight. We configured all three detectors identically, and set them to begin recording when ultrasonic signals were detected and to continue recording for 10 s, or as long signals were present. Approximate height of detectors at start of recording sessions was calculated using a Bushnell Sport 450 Laser Rangefinder (Bushnell Corporation, Overland Park, KS, USA). Altitude estimates were generally conservative as the Helikite tended to rise slightly during recording sessions as winds picked up after sunset.

We tested bat response to possible migration events by deploying the Helikite during or after passage of cold fronts on nights with northerly winds. To evaluate relative foraging activity by altitude and moth density, we performed a t-test of proportion of activity at altitude vs ground level. Altitude was modeled as both a two-level factor (Helikite-based detectors or ground level detector) and a three-level factor (high = upper Helikite detector at 200m, medium = lower Helikite detector at 100m, and low = ground-level detector.) We also deployed the Helikite on 2 nights with southerly winds to document bat behavior outside of possible migratory event conditions.

Echolocation Call Analysis

We used Kaleidoscope software (v 0.1.8, Wildlife Acoustics Inc., Concord, MA, USA) to extract echolocation call files from compressed recordings, where each file included a series of echolocation calls representing a pass by one or more bats (Sherwin et al. 2000) which triggered a recording. Sonobat software (v 3.1.4 West, Sonobat, Arcata, CA, USA) provides quantitative quality assessments of

bat calls in addition to probability of species identification. We used it to identify files containing high quality calls (80% quality or higher), to identify calls to bat species where possible, and to generate call parameter data on the highest quality calls in each call file. We only included files confirmed by Sonobat as containing only calls of Brazilian free-tailed bats. Some call files represented passes by multiple individuals, particularly during periods of high insect activity. Because it was not possible to accurately determine the number of bats contributing to each sequence, we conservatively considered each call file to represent a single bat pass (Sherwin et al. 2000). Feeding was defined as the presence of one or more “feeding buzz” call sequences (Hayes 2000) in a pass, as identified by listening to time-expanded recordings. Calls that appeared to represent social interactions or had incomplete “feeding buzz” sequences were not included in the analysis of feeding activity. We performed t-test analyses using JMP (v 10.0, SAS Institute Inc., Cary, NC, 1989-2013).

To evaluate differences in echolocation call parameters attributable to altitude and moth explanatory variables, we retained only call files containing high-quality search phase calls typical of Brazilian free-tailed bats (Figure 1). The long duration, constant frequency (CF) calls used by these bats are effective for detecting prey in uncluttered areas (Schnitzler and Kalko 2001). We used this conservative approach to ensure validity of comparisons between altitudes and moth density levels. We used the following call parameters as defined by the Sonobat software: Duration (ms), high and low frequency, the highest and lowest apparent frequencies of the call (kHz), and characteristic frequency (Fc), the frequency at the point in the final 40% of the call having the lowest slope or exhibiting the end of the main trend of the body of the call (kHz). Finally, we calculated the mean of each call parameter for up to eight highest quality calls, based on Sonobat quality ratings, in each call file.

Call parameters were standardized using z-transformation because they represented different types of measurement units and to meet the requirements for canonical ordination. We analyzed the transformed call parameter data using the “vegan” (Oksanen et al. 2013) package in R (R Core Team, 2013; v 3.0.1, Macintosh). We used the “rda” function to perform a Redundancy Analysis (RDA) following Borcard et al. (2011). RDA combines multiple regression with classical ordination and is useful for explicitly examining the relationships between multiple explanatory variables and a response matrix. RDA thus describes the proportion of variation in a dataset directly attributable to a set of explanatory variables in constrained space. We used altitude and moth levels, each modeled as three-level factors, as explanatory variables, and call parameters as response variables. We tested the significance of the canonical ordinations with permuted ANOVA tests (1,000 permutations).

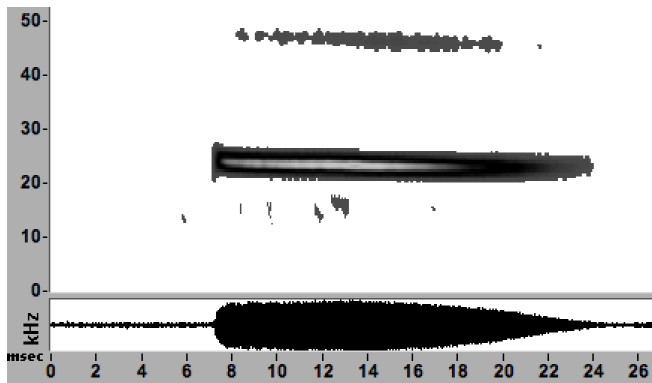


Figure 3.1. Sonogram of bat search phase call.

Sonogram of a representative *Tadarida brasiliensis* search phase call as recorded using an SM2Bat detector in real time expansion mode, with call frequency (kHz) on the Y axis and time (ms) on the X axis. Higher amplitude within the call is represented with lighter shading, and the horizontal window at the bottom represents overall amplitude. The faint harmonic above the main call indicates that no higher frequencies were lost in the main call. This call was recorded on Oct 18, 2012, Uvalde Co., TX, at an altitude of approximately 200m AGL. Sonogram produced using Sonobat software.

Results

We conducted recording sessions during 13 nights between Aug 29 and Oct 19, 2012 (Figure 2). Mean recording duration was 2.64 h. Recordings documented bat activity in relation to six cold fronts passing over the study area on Sept 7, 13, 18, 29, and Oct 5 and 17. Three of the cold fronts, Sept 18 and 29 and Oct 5, were also associated with strong peaks in number of moths in pheromone traps, and thus likely represented moth migration events (Figure 2). We were only able to gather data on the day of frontal passage for the Sept 18 event, not following days, and moth numbers did not begin to peak until the following days when conditions were not suitable to fly the Helikite. The night of Sept 14 was anomalous with high bat activity yet no evidence of a moth migration event or local emergence, and was thus excluded from further analysis. Detector altitudes varied with wind conditions, but were 100 ± 22 m (lower Helikite detector) and 200 ± 36 m (upper Helikite detector) AGL. We recorded a total of 1,784 bat passes, of which 1,104 were confirmed by Sonobat software as belonging to Brazilian free-tailed bats. In addition, we recorded calls identified as from *Eptesicus fuscus*, *Eumops perotis*, *Lasiurus blossevillii*, *Lasiurus cinereus*, *Lasionycteris noctivagans*, *Perimyotis subflavus*, and *Myotis spp* (assumed to be mostly *M. velifer*). Remaining bat passes were not attributable to a single species or contained calls from multiple species.

Brazilian free-tailed bat foraging activity was greater during moth migration events ($t = 2.50$, $DF = 18.7$, $p = .02$) and greater at ground level than above ground level ($t = 1.88$, $DF = 10$, $p = 0.0445$), but was not significant proportionally higher at higher altitudes during moth migration events than at lower levels of moth activity. Feeding buzz activity also varied significantly with altitude ($t = 1.82$, $DF = 14.02$, $p = 0.045$) but not level of moth activity.

We evaluated parameters from high-quality search phase calls from 180 bat passes at the upper Helikite detector, 221 bat passes at the lower Helikite detector, and 377 bat passes at ground level. The amount of variation in call parameters attributable to altitude and moth density was significant in the overall RDA model ($DF = (4, 537)$, $F = 47.83$, $p = 0.001$, $r^2_{ADJ} = .26$), and the first two RDA axes were significant (RDA1: $DF = (1, 537)$, $F = 185.43$, $p = 0.001$; RDA2: $DF = (1, 537)$, $F = 5.26$, $p = 0.012$). The first axis explained 25.5% of all variation in call parameters, and primarily reflected differences due to altitude; call duration increased with altitude, and all three frequency-related parameters decreased with altitude (Figure 3.3, Table 3.2). The slight but significant portion of the variation explained by moth levels holding variation due to altitude constant (1%, $DF = (2, 537)$, $F = 5.57$, $Pr(>F) = .019$, Figure 3.4) was represented by factor loadings showing all call parameters decreasing at the highest level of moth activity.

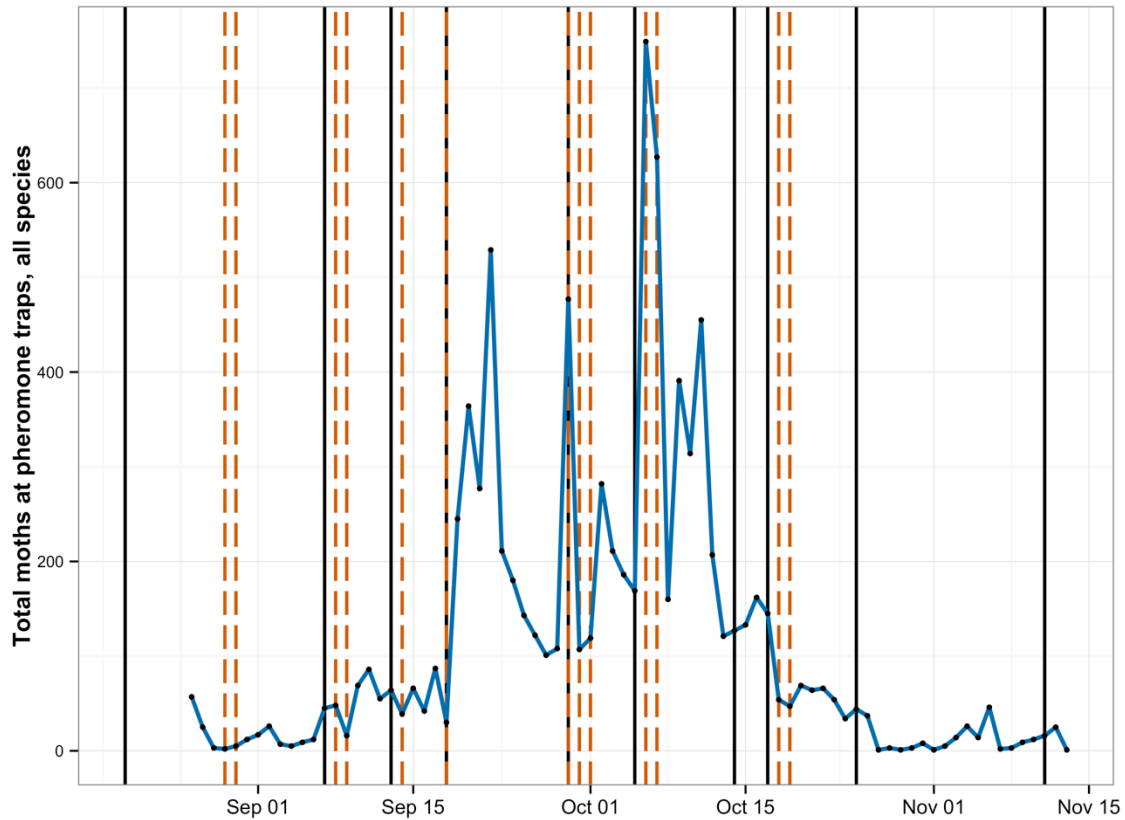


Figure 3.2. Helikite data collection nights.

Total numbers of five species of migratory noctuid moths captured at pheromone traps in the study area (Uvalde Co, Texas, USA) between late Aug and mid Nov 2012. Solid black vertical lines represent cold front passages, which often resulted in winds favorable for moth migration events. Dashed red vertical lines represent nights when acoustic data was captured for this study. Moth migration events (high moth activity) were associated with cold fronts on Sept 18, 29, and Oct 5.

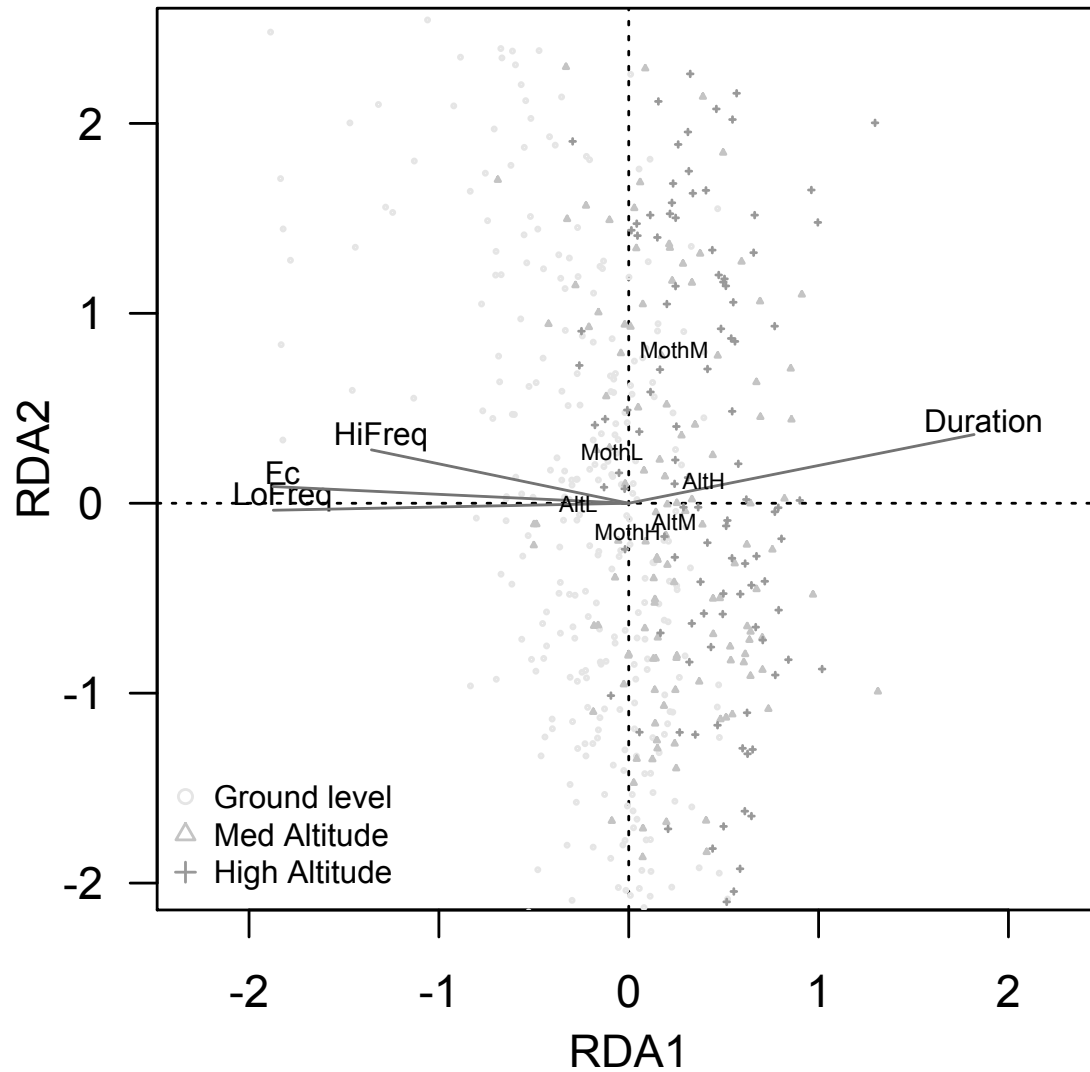


Figure 3.3. RDA axes explaining call parameter changes overall.

Plot of the first two axes of the Redundancy Analysis showing the call parameters responsible for 21.8% of variation in Brazilian free-tailed bat search-phase calls due to altitude and moth activity, and the centroids of those explanatory variables. Angles represent correlations, but distances do not approximate Euclidean distances. Most variation is due to call duration increasing and call frequency decreasing with altitude

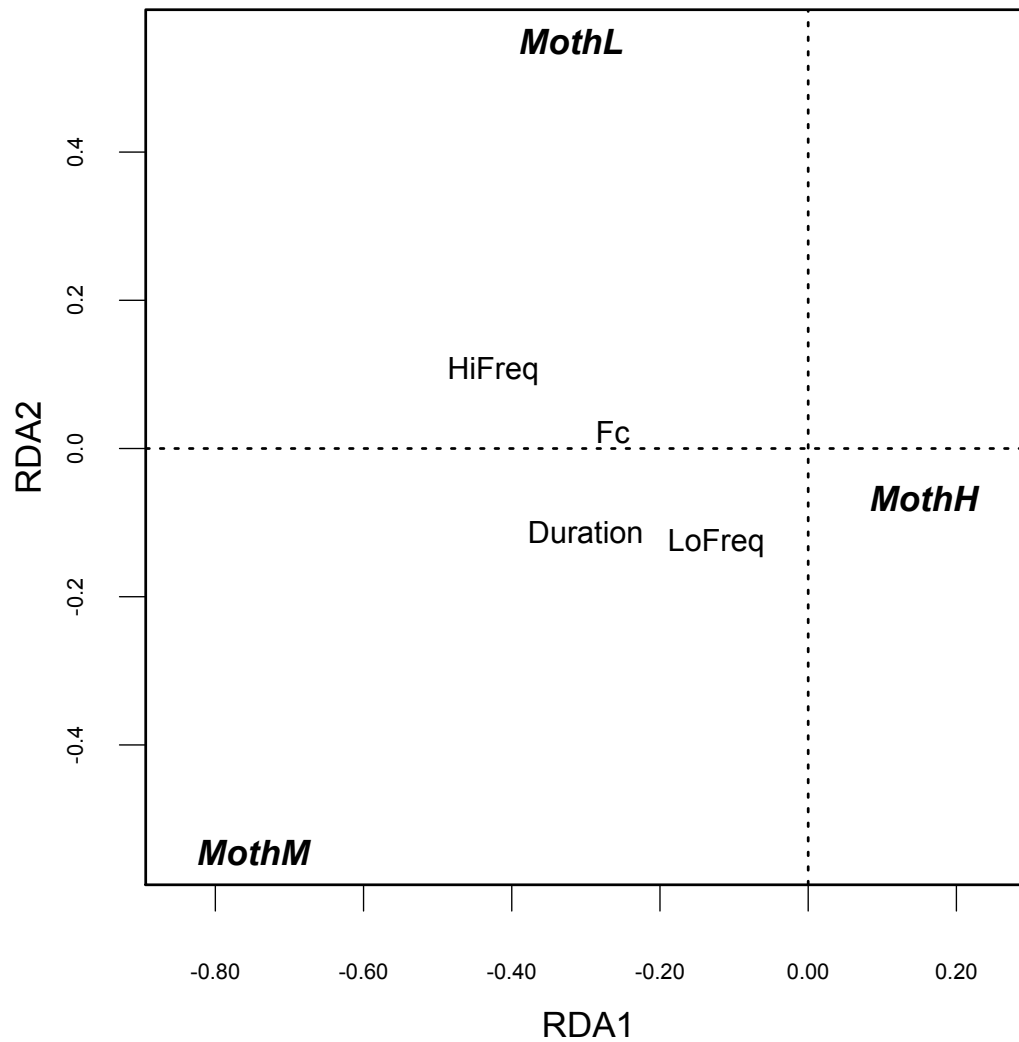


Figure 3.4. RDA axes explaining call parameter changes due to moths.

Plot of the first two axes of the Redundancy Analysis showing the call parameters responsible for 1% of variation in Brazilian free-tailed bat search-phase calls due to moth activity, and the centroids of those explanatory variables. Angles represent correlations, but distances do not approximate Euclidean distances. All call parameters decrease at high levels of moth activity

Table 3.1a. Brazilian free-tailed bat activity at different altitudes and levels of moth activity

Recording Date	Moth Migr.	Bat passes Ground	Bat passes Low Kite	Bat passes High Kite
Aug 29	0	70	8	7
Aug 30	0	22	25	2
Sept 8	0	4	0	2
Sept 9	0	17	4	9
Sept 14 ⁺	0	57	101	66
Sept 18	0	10	8	21
Sept 29	1	73	25	30
Sept 30	1	40	9	12
Oct 1	1	174	60	46
Oct 6	1	18	16	7
Oct 7	1	64	45	27
Oct 18*	0	n/a	7	14
Oct 19*	0	n/a	2	2

Table 3.1b Bat feeding buzzes at varying levels of altitude and levels of moth activity

Moth Migration	Total bat feeding buzzes		
	Ground	Low Kite	High Kite
No	10	1	3
Yes	25	12	6

Foraging (a) and feeding (b) activity of Brazilian free-tailed bats represented as total number of call files recorded in the study area (Uvalde Co, Texas, USA) during fall 2012 at varying levels of altitude and moth activity. *Ground-based detector not functional on these dates + Data from this date excluded from activity and feeding buzz analysis as an outlier. See text for details

Table 3.2 RDA call parameter loadings

	Full Model	Alt only	Moth only
Parameter	RDA1	RDA1	RDA1
Duration	1.869	1.723	-0.3002
Fc	-1.824	-1.782	-0.2637
LoFreq	-1.822	-1.796	-0.1239
HiFreq	-1.305	-1.289	-0.4251

Factor loadings for Redundancy Analysis results using z-transformed call parameter data, with loadings scaled proportional to eigenvalues. For the full model, significant loadings include the first two axes. The first axis explains 25.5% of search-phase call parameter variation due to altitude and number of moths. For the model explaining variation in call parameters due to altitude, holding moth levels constant, significant loadings in the first axis explain 24% of all variation. For the model explaining variation due to moth level, holding altitude constant, the significant loadings in the first axis explain 1% of all variation.

Discussion

This is the first study to directly link high-altitude foraging behavioral responses of bats to insect migration events. Our results show that Brazilian free-tailed bats forage more at higher altitudes in response to higher levels of migratory moths. We also found that bats change echolocation parameters in response to altitude and moth levels, which supports earlier studies demonstrating similar shifts in duration and frequency of bat echolocation calls at different altitudes (Gillam et al. 2009).

Large numbers of insects migrate southward in the fall at higher altitudes with favorable winds, directly following the leading edge of cold front passage in the Central Texas area (Beerwinkle et al. 1994, 1995, Krauel and McCracken, unpubl. data). While insect migration events involve vast amounts of biomass, they are spread out over time and in three-dimensional space, with density no more than 103 to 104 insects per 106m³ (Beerwinkle et al. 1994, Pedgley 1990). Direct sampling of insects aloft is difficult, expensive, and often frustrating (Westbrook 2008). However, an earlier study showed that noctuid moth captures in ground-level pheromone traps in the study area closely matched radar documented mass movement of moths, especially in the fall (Beerwinkle et al. 1995). We found significantly more bat activity at higher altitudes when numbers

of moths in pheromone traps were at medium and high levels. Thus, our results support the use of ground-level pheromone traps and weather data to model fluctuations in prey density aloft.

While pheromone trap numbers were useful for predicting differences in bat activity with altitude, we observed one anomalous recording night that did not fit the pattern. Sept 14 was one day after a cold front passed through the study area. However, pheromone trap data did not suggest a concurrent migration event (Figure 3.2). In addition, pheromone trap data from northerly locations that might have served as sources of migratory moths on that night also do not support a migration event (J. Westbrook, pers comm). Nonetheless, our data show high amounts of bat activity, especially above ground level. It is possible that the activity represented a local emergence event. Corn earworm moths can show variable response to black light traps upon emergence (Lopez et al. 1979), but we saw no evidence of this in our pheromone and black light trap pairs. Finally, insects caught in a black light trap co-located with the Helikite flight do not indicate a local emergence of large numbers of other insects. Thus we regarded data from Sept 14 as an outlier and did not include it in our analysis.

Earlier studies recorded echolocation calls at higher altitudes than examined in this study (McCracken et al. 2008, Gillam et al. 2009). However, we found that differences in bat foraging patterns and echolocation call parameters were still evident at approximately 100 m and 200 m. This may be due to weather patterns favoring lower migratory altitudes for moths in fall than in spring. During spring migrations, insects use fast-moving nocturnal jets at altitudes of 400 m to 1500 m AGL to assist long-distance movements of up to several 100 km/night (Showers et al. 1989, Wolf et al. 1990, McCracken et al. 2008). In contrast, movements in fall tend to be at lower altitudes and in slower winds (Wolf et al. 1990, Showers et al. 1993, Beerwinkle et al. 1994). For example, black cutworm moths were found at 100-300 m AGL during the fall (Showers et al. 1993), and Beerwinkle et al. (1994) observed peak flows of migrating insects at 200 m AGL following passage of a cold front in Sept.

Most of the altitude- and moth level-specific variation in echolocation call parameters (RDA axis 1, Table 3.2, Figure 3.3) was likely related to altitudinal differences, because the altitude centroids were dispersed primarily along the RDA1 axis (Figure 3.3). In addition, a partial RDA on altitude holding moth levels constant was significant, explained 24% of all variation, and showed very similar loadings in call parameters (Table 3.2). As in earlier studies, bats tended to use search phase calls with longer duration and lower frequency at higher altitude (Gillam et al. 2009). Brazilian free-tailed bats have a very flexible echolocation repertoire (Gillam and McCracken 2007) and are able to use calls with short duration and greater bandwidth to detect smaller prey or avoid collisions in situations such as ground-level background clutter (Kalko and Schnitzler 1993,

Gillam and McCracken 2007). At higher altitudes and away from background clutter, free-tailed bats can use longer duration and lower frequency to receive information over greater distances and subject to less attenuation (Gillam et al. 2009).

Unlike the previous study, however, we also considered possible changes in echolocation call parameters due to differences in prey levels. The amount of variation due specifically to differences in numbers of moths was 1%. This small but significant variation was related to decreases in call frequencies and duration with higher moth levels. In areas of higher prey density, bats would not need to search over great distances, and could use calls of shorter duration regardless of altitude. Target migratory moths tended to be larger than many other insects found in black light traps during this study (pers obs). The observed negative correlation between echolocation frequency used in calls and level of migratory moths could be explained by the presence of larger prey, requiring less frequency modulation to detect in search phase calls.

Despite the magnitude of resource fluctuations across the landscape during insect migrations, much of it is overlooked due to lack of research on such movements at higher altitudes (Diehl 2013). Seasonal migrations of insects occur primarily at night, and have been documented everywhere they have been looked for (Drake and Gatehouse 1995). During migration, moths often fly in layers representing favorable temperature and wind direction (Chapman et al. 2008a, 2008b), resulting in higher concentrations of insects that might be more easily detected by bats. Brazilian free-tailed bats track resources in time and space (McCracken et al. 2012) and are known to forage at high altitudes (Williams et al. 1973, Griffin and Thompson 1982, McCracken et al. 2008, Gillam et al. 2009). It is therefore reasonable to expect that a large number of moths migrating through an area would attract bats. We have shown that this is likely the case for Brazilian free-tailed bats and the fall migration of noctuid moths. We expect this phenomenon to be more widespread than this particular study system. Interactions between predators and migratory prey are poorly documented yet important pieces of our ecosystem that face challenges due to loss of habitat and climate change.

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CONCLUSION

Integrative studies of migratory animals, especially those including multiple taxa or trophic levels, are important and yet challenging to conduct (Bowlín et al. 2010). This dissertation considers a system of migratory insects and the migratory bats known to prey on them. The system itself is important because the moths are destructive agricultural pests affecting crops on a continental scale, and the bats offer significant pest control ecosystem services (Cleveland et al. 2006; Federico et al. 2008). In addition, understanding the system is important because it is weather-driven and thus likely to be affected by climate change (Parmesan and Bi 2001; Sparks et al. 2007; Newson et al. 2009; Robinson et al. 2009; Bale and Hayward 2010).

In this study, I tested the following hypotheses:

1. Changes in noctuid moth numbers are linked to changes in regional and local meteorological patterns
2. Bat flight activity and changes in body mass are linked to the same weather patterns
3. Bats alter foraging patterns to take advantage of increased levels of migratory moth abundance
4. Bats shift echolocation call parameters with altitude and levels of migratory moth abundance

Noctuid moth migrations during the 2010-2012 fall seasons were driven significantly by weather at the regional and local levels. Bats also responded to the same weather patterns. I documented changes in body mass, duration of foraging time at the cave, foraging activity levels at different altitudes, and echolocation call structure to increased northerly wind after cold front passage. Many of the behavioral and physiological changes in bats were more likely due to their own migratory cycles, rather than in direct response to the local availability of migratory moths in the study area.

The overall effects of animal migratory movement at a landscape scale are likely to be significant (Bauer and Hoye 2014). Migrants may spend little time in each community along their migratory routes, but they may alter each of those communities by contributing or consuming resources such as nutrients or pathogens (Bartz and Naiman 2005, Altizer et al. 2011) or by taking a transient role as predator or prey (Sanchez-Zapata et al 2007, this study). Weak interspecies interactions, where one species has a mild effect on the population of another species, can stabilize complex food webs (McCann et al. 1998; Rooney and McCann 2012). Such stabilizing mechanisms include dampening oscillations in consumers or resources, and migrant animals can function in this manner if they are only present during times of high or low abundances. In

addition, the transient nature of migrants can prevent strong interactions with residents, resulting in prey switching when migrants appear, offering a further stabilizing effect (McCann et al. 1998; Rooney and McCann 2012).

However, few theoretical models include the effects of migrants in community assemblages or food webs (Bauer and Hoyer 2014). In this study, migratory noctuid moths provide a high quality resource for bats during a time when local primary production, and thus the local insect population that depends upon host plants, are greatly reduced from spring and summer levels. This is an example of a migratory animal dampening an oscillation of resource availability, and it may enable bats to remain in the area longer than would otherwise be possible. Future analysis of bat prey from guano collected during this study will document the extent that bats exploit this resource during the fall season and the role of migratory moths in changes in bat prey community over time.

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VITA

Jennifer Krauel received a Bachelors of Science degree in Business Administration with a major in Information Technology from California State Polytechnic University in Pomona, California, in 1982. She worked in various capacities in the computer software business from 1982 until 2005 at Hewlett-Packard, Oracle, and Actioneer, Inc. She completed her Masters in Science degree with a major in Ecology and Systematics at San Francisco State University in 2009. She graduated with a Doctors of Philosophy degree from the University of Tennessee, Knoxville, in the department of Ecology and Evolutionary Biology in Summer 2014.